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PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON

152nd Session (1939–40) Part 3

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PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

152nd Session (1939–40) Part 3

PROCEEDINGS OF THE GENERAL MEETING
14 March 1940

Mr. J. Ramsbottom, O.B.E., M.A., Dr.Sc., President, in the Chair

The Proceedings of the General Meeting held on Thursday, 29 February 1940, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The President referred to a collection of paintings of flowering plants, mainly British, recently bequeathed to the Society by Major Joshua Reynolds Gascoigne Gwatkin, of The Manor House, Potterne, Devizes, who died on 12 September 1939. The collection numbers about a thousand paintings.

Major Gwatkin, who was a collateral descendant of Sir Joshua Reynolds, P.R.A., was born 24 March 1855. He was a M.A. of Cambridge, and became J.P. for the County of Wilts in 1889. In 1887 he became a Captain in the Royal Wilts Yeomanry, and later a Major. Devoted to hunting and shooting, he was a Member of the British Ornithologists' Union, and was skilled in setting up specimens of birds in their natural surroundings. His flower paintings, which were the work of many years, show a happy combination of botanical knowledge and artistic skill. Most of them have the plant habitats noted, and in some cases other notes have been added. The paintings are arranged in the sequence of the British Flora, with the exception of the Umbelliferae, which are kept in a separate volume.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted :—Walter Eric James.

The following candidates were balloted for and elected Fellows :—Marian Muriel Whiting, Sir Geoffrey Evans, C.I.E., M.A., Walter John Zimmer, Thornton Horace Hawkins, Richard Clements and Allan Eslick, B.Sc.

The President reported the deaths of the following members :—Dr. T. W. Woodhead and Dr. R. T. Gunther, Fellows ; and Mr. H. Stuart Thompson, Associate.

The President welcomed the presence of Dr. Roger Heim, the first of France's representatives in the scheme of scientific co-operation.

Miss M. S. Campbell, F.L.S., who since 1938 has represented the Society on the Phenological Committee of the Royal Meteorological Society, gave a report on the work, to which Major H. C. Gunton, M.B.E. (Visitor), added some remarks.

Report by Miss Campbell.—

For about fifty years Phenological observations have been made under the auspices of the Royal Meteorological Society to elucidate more exactly the relations between meteorology and seasonal events, that is between cause and effect. For this purpose the Royal Meteorological Society prepared lists of plants, birds and insects, suitable for observations throughout the British Isles. Voluntary observers—they number about four hundred at the present time—in various parts of the country, obtain a specially prepared form from the Society, and fill in details as to when a certain plant comes into flower and when a certain bird, butterfly or moth makes its first appearance. With plants particular care is taken to observe the same individual each year, as far as possible. Notes as to exceptional weather, and other relevant matter, are encouraged. Observers are also invited to give details of the habitat of the plants as regards their degree of exposure and the direction of any shelter. In addition to the voluntary observers a number of research stations assist in supplying data.

In 1937 Major Gunton undertook to revise and organize the work and to put it on a more scientific basis. Scientific Institutions and Societies were invited to send representatives to serve on a main conference and executive committee. This Society has been represented since November 1938, and in addition to the main conference and executive, I have been appointed to the newly formed botanical panel. As I serve as a botanist I will give a few details of the work of revision in the botanical section.

Various items in the plant list obviously called for revision.

There appeared to be some confusion as to the identity of *Scabiosa Succisa* because of its English name of Devil's Bit. Observers who were not familiar with the latin name confused it with Sheep's Bit, which is the quite unrelated *Jasione montana*. We therefore decided to remove it from the list. The other plant that we have expunged is *Centaurea nigra* because, as its name covers several species and forms which have different flowering times, the data received were therefore very unsatisfactory. *Rosa canina* is suspect for the same reason—the species likely to be observed in the north of Scotland, for example, is probably not the same as that observed in the south of England, so that one would not expect comparison of the first flowering dates to signify very much. Curiously enough, however, "*Rosa canina*" appears, from the data acquired, to give some of the most satisfactory results! Not being a rose specialist I am not prepared to offer an explanation of this, but it suggests that all ordinary pink wild roses have the *same* flowering time.

During this season we are hoping to test possible substitutes for these dubious species and are inviting additional observations on such plants as the Foxglove. It did not seem desirable to introduce substitutes to the list without some experiment as to their phenological usefulness. For one thing it is essential that the new plant should have an average flowering time approximate to that of the plant it is to replace. If the substitute does not fit into the gap, the curve drawn to illustrate the nature of the season, by joining the times of appearance of the series of species observed (the species are supposed to be in order of appearance), would be much disturbed. Consider, for example, a curve drawn in conjunction with numbers one to twenty; if numbers five and fifteen were to change places there would be a violent and erratic deviation in the curve.

Nomenclature in all groups is also undergoing revision and being brought up to date.

Each year Major Gunton analyses all the observers' returns and draws diagrams to illustrate the results in their relation to temperature, rainfall and sunshine recordings. This information is included in the annual report which is published as a part of the 'Quarterly Journal of the Royal Meteorological Society'.

As regards the results, much of course depends on the season: 1938 was an unusual one with very marked cold and warm spells. When the observations were analysed the results of these spells confirmed ideas as to the existence of certain principles of phenology which in less marked seasons tend to be obscured. The cold and warm spells have different effects on the same species in different parts of the country. To take

an imaginary case : consider two places so far apart to north and south that their average times of flowering differ by ten days. In the south the plant may be held up for a week by a cold spell which only slightly affects the less advanced growth further north. A warm spell following may then bring out the plant in the north a few days ahead of its average time, so that the plant may then be flowering in north and south at the same time. On the contrary, a warm spell may bring out the plant in the south five days ahead of its time, that is fifteen days before the flower is due in the north, and then near that time a cold spell may delay the northern plant for a week so that the difference in flowering between north and south is three weeks. This is merely an outline of an interesting and important point, and I hope that Major Gunton, who is here this afternoon, will show you a diagram and give you further details.

The results for 1939 are not yet available, so I am not able to give any information about them. The need for economy necessitates the cutting down of the Report but we hope to be able to retain all the essential features.

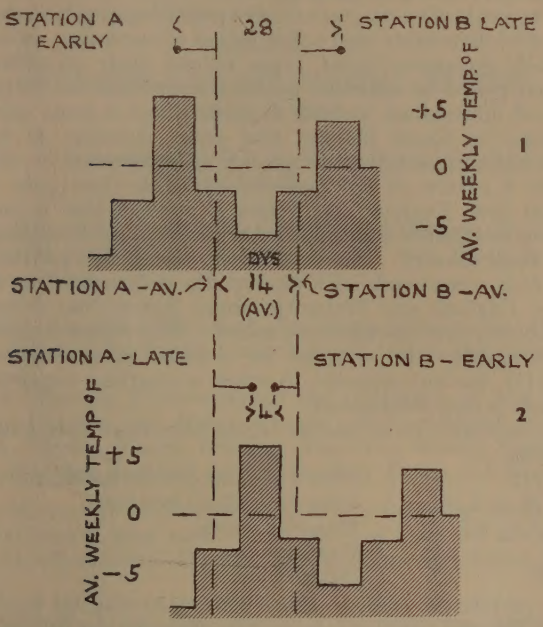
Copies of the forms which are used by observers are on the table for the benefit of those interested, and I should like to add that new observers would be very welcome.

Major H. C. Gunton said how much the Royal Meteorological Society appreciated the representation of this Society on their Phenological Committee and the assistance already contributed by Miss Campbell.

He referred to the complexity of the factors which determined the dates of the events, such as the flowering of plants or the emergence of insects, with which they had to deal, and which included specific and site characteristics, the weather during a considerable period in advance and the weather of the moment. If the dates for a particular year were compared with the corresponding average dates, it would be seen that there were marked departures from the average relationships not only as regards the same item at different stations, but also as regards different items at the same station. This is due to the influence of the incidence of warm and cold spells in relation to the average dates, as illustrated by the accompanying figures.

Figs. 1 and 2 illustrate the cases of two Stations A and B at which the average dates for a particular item differ by 14 days. In the situation illustrated by fig. 1 Station A becomes early and Station B late, the difference in date becoming 28 days. In the situation illustrated by fig. 2 Station A becomes late and Station B early, the difference

in date being 4 days. The difference in the incidence of the warm and cold spells has thus caused a total variation of 24 days.



Diagram, in two figures, showing how earliness or delay in the arrival of weather with two spells of stimulating temperatures may cause Stations A and B, on the average 14 days apart, to be 28 days apart (fig. 1) or only 4 days apart (fig. 2).

Dr. H. Godwin (Visitor), gave an account, illustrated with lantern-slides, of ' Pollen analysis and the Forest History of England and Wales '.

Abstract.—

Since the summary presented by Erdtman in 1928 of the results of his investigations in the British Isles (' Studies in the postarctic history of the forest of north-western Europe, I.—Investigations in the British Isles '. Geol. Fören. Stockholm Förhandl. LVI/2, pp. 123–92 ; 1928), the pollen-analysis technique has been applied to many more sites, and many aspects of post-Glacial change. It is now opportune to review the advances which have been made in application of the

method to England and Wales and to enquire firstly, how far a convincing scheme of forest history has emerged, and secondly, how far such a scheme has been linked with climatic, archaeological and geological indices.

The typical pollen diagram for the post-Glacial period shows a threefold divisibility into a first period of increasing warmth, in which successive forest types extend their importance, a second period of optimum forest-development, and a third period of diminishing warmth in which there is some sign of revertence in forest history, and some extension of trees (beech and hornbeam) not previously of importance.

From a review of the evidence available from sites distributed over England and Wales it appears that a pollen zonation established in the East Anglian Fenland is applicable to the whole country. This reveals a strong regional differentiation which corresponds with present day differences ; in each part of England and Wales the forest history has followed an equivalent but not identical course. This regional parallelism strengthens the evidence for a phase of revertence in zone VIII, the Sub-Atlantic, in which a returning importance of *Betula* is very widespread.

The successive zones and sub-zones have been distinguished as follows :—

VIII	Alder-Oak-Elm-Birch-(Beech) zone.
VII (*a* & *b*)	Alder-Oak-Elm-Lime zone.
VI (*a*, *b* & *c*)	Pine-Hazel zone.
V	Pine zone.
IV	Birch-Pine zone.

The correlation of these zones with archaeological horizons in the Fenland can be consistently extended to the rest of England and Wales. There are three good correlations of the Mesolithic with zones V and VI, one Neolithic correlation with the middle of zone VII, one Romano-British correlation in zone VIII, and a series of Bronze Age and Early Iron Age correlations with the end of zone VII or the transition between zones VII and VIII. It is clear that the Bronze Age and Iron Age correlations in particular call for closer investigation.

Pollen-analysis has been applied with success to determination of the age of the submerged peat-beds round our coasts. Moorlog from the deep parts of the North Sea is referable to zones IV and V, and on the coast of South Wales peaty layers between −55 and −28 ft., O.D., belong to the second half of zone VI, thus showing the end of a phase of rapid and extensive marine transgression. It should be possible to employ the pollen-analysis method to resolve the isostatic and eustatic components of land and sea-level movements, and it will certainly shed light on the former distribution of both fauna and flora.

Mr. H. G. Maurice, C.B. (Visitor), gave an account of 'The rational exploitation of the Sea'.

The President expressed the thanks of the Society to the speakers at the present Meeting.

PROCEEDINGS OF THE GENERAL MEETING
11 April 1940

Mr. J. Ramsbottom, O.B.E., M.A., Dr.Sc., President, in the Chair

The Proceedings of the General Meeting held on Thursday, 14 March 1940, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted:—Allan Eslick, Marian Muriel Whiting, Thornton Horace Hawkins, Mary Rebekah Lambert and Sir Geoffrey Evans, C.I.E.

Certificates of recommendation of the following candidates for Fellowship were read:—For the first time, in favour of Donald Albert Coult, Francis Charles Fraser and Kailas Nath Kaul.

Certificates of recommendation of the following candidates for Foreign Membership were read for the first time:—Prof. August Adriaan Pulle, of the University of Utrecht, and Dr. Thomas Barbour, of the Museum of Comparative Zoology, Harvard College.

The following Fellows were elected as Auditors of the Treasurer's accounts for 1939–40:—Representing the Council—Miss M. L. Green, Mr. H. R. Hewer; Representing the Fellows—Mr. D. J. Scourfield, Dr. T. A. Sprague.

The President announced that the Council had resolved unanimously to award the Linnean Gold Medal for 1940 to Sir Arthur Smith Woodward, F.R.S., and the Crisp Award and Medal to Mr. D. J. Scourfield, I.S.O.

Dr. V. J. Chapman, F.L.S., read a paper, 'The functions of the pneumatophores of *Avicennia nitida*'. [Printed in full, overleaf.]

Prof. R. R. Gates added some remarks.

'A Discussion on Phylogeny and Taxonomy' was held as a Joint-Meeting with the Association for the Study of Systematics in relation to General Biology.

After Mr. J. S. L. Gilmour, Dr. O. W. Richards, Dr. T. A. Sprague and Dr. E. I. White had contributed short papers, the following took part in the discussion,—Dr. H. Hamshaw Thomas (his remarks being read by Mr. Gilmour), Dr. Julian Huxley, Dr. W. B. Turrill, Sir William Wright Smith, Dr. R. Melville, Mr. B. L. Burtt, Dr. J. Burtt Davy, Mr. M. J. D. White, and the President. [Printed below, p. 234.]

The following papers were read in title :—

'Some Nemerteans from South Africa and a note on *Lineus corrugatus* M'Intosh'. By J. G. F. Wheeler, D.Sc., F.L.S. [Printed in the Journal, Zoology, xli, p. 20.]

'The seasons in a tropical rain-forest (New Hebrides). Part 5. Birds (*Pachycephala*)'. By John R. Baker, D.Sc., A. J. Marshall and T. H. Harrisson. (Communicated by Prof. E. S. Goodrich, F.R.S., F.L.S.) [Printed in the Journal, Zoology, xli, p. 50.]

THE FUNCTIONS OF THE PNEUMATOPHORES OF AVICENNIA NITIDA Jacq.

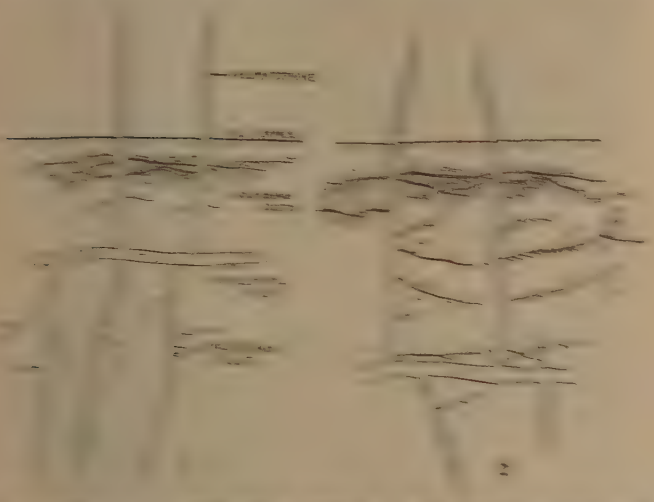
By V. J. Chapman, Ph.D., F.L.S.

A study of the pneumatophores of *Sonneratia alba* by Troll and Dragendorff ('Planta', xiii, p. 311 ; 1931) showed that these organs carried out two other functions in addition to providing a means of gaseous exchange. These other functions were

(*a*) respiration,

(*b*) the maintenance of the lateral absorbing rootlets just below the soil surface, fresh rootlets appearing at successively higher levels on the pneumatophores as the soil surface rose because of silt deposition. This function is probably as important as that of gaseous interchange.

One of the objects of the Cambridge University Expedition to Jamaica last summer was to try to determine how many of these three functions were carried out by the pneumatophores of *Avicennia nitida*. As it seems unlikely that a full and detailed account of this work can appear in the near future a brief note on the results of this aspect of the Expedition's work may not be amiss. The Expedition was financed by a number of bodies, but it was the grant from the Royal Society that originally made the visit possible, and our thanks are primarily due to that body and also to others who assisted.



It is at once obvious from these figures that the composition of the gas obtained from these swamps is very far removed from that of the atmosphere. The oxygen content is much lower—usually less than half—whilst the carbon dioxide content is much higher. Although there is some oxygen available in the soil-atmosphere it is very doubtful whether

TABLE I.

Site.	Soil.	% CO_2.	% O_2.
Avicennia glade	peat.	6·26	9·61
Area of dead *Avicennia*	sand.	0·11	2·69
Swamp, Hunts Bay	mud.	0·12	0·0
Swamp, up Rio Cobre	mud.	7·24	6·76
Swamp, up Ferry River, with some freshwater vegetation .	mud.	11·53	21·59
Single tree	sand.	4·47	2·45
Avicennia fringe	sandy mud.	8·08	5·67
,, ,, ...	,, ,,	9·17	3·65
,, glade	peat.	11·53	8·09
,, ,, ...	peat.	5·31	6·26
,, Carenning Is.	peat.	10·74	7·80
Edge of swamp, Port Royal ..	peat.	4·97	5·16

the concentration could be regarded as adequate for respiration. Furthermore, there is the difficulty of penetration through the periderm of the lateral roots since the lenticels are confined to the erect pneumatophores.

The Pneumatophores.—The next step in the investigation was an analysis of the gas contained within the pneumatophores and lateral roots. Samples of gas could be readily expressed from these organs, collected and analysed. The results are shown in Table II.

TABLE II.

Site.	Soil.	Organ.	% CO_2.	% O_2.
Pool, Rio Cobre ..	mud.	Pneumatophore.	1·65	19·12
,, ,, ..	,,	Horizontal root.	1·62	19·18
Beach, Hunts Bay.	sand.	Pneumatophore.	0·11	20·58
Wet depression ..	mud.	,,	0·97	19·76
Avicennia fringe. .	sandy mud.	,,	0·32	20·03
,, ,, .	,, ,,	Horizontal root.	1·24	18·94
Open salina	sand.	Pneumatophore.	1·12	18·95
,, ,, ...	,,	Horizontal root.	1·57	18·20
Swamp centre ...	peat.	Pneumatophore.	1·30	19·64
,, ,, ...	,,	Horizontal root.	0·70	19·12

Two points at once emerge from these figures.

(1) There is no fundamental difference between the composition of gas in the pneumatophores and that in the horizontal roots. Troll and Dragendorff, on the other hand, found that there was a gradual increase in the CO_2 concentration the greater the distance from the pneumatophore.

(2) The composition of the gas is very close to that of the atmosphere and is very different from that of the soil gas.

It may therefore be concluded that, although some of the necessary oxygen may be obtained from the soil water and soil atmosphere, nevertheless the bulk of the gaseous exchange must take place by way of the pneumatophores, and that this is one of their primary functions.

Experiments were also carried out to determine the difference between lenticular and cuticular exchange in the pneumatophores. In these experiments the lenticels were inhibited from functioning by treatment with chloroform. The results showed that the bulk of the gaseous interchange took place through the lenticels but that there was some

TABLE III.

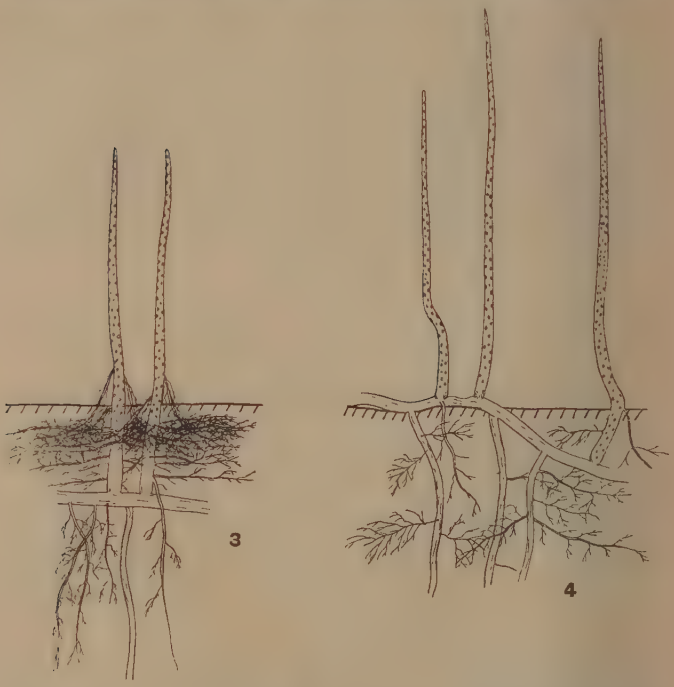
Organ.	% gas admitted into gas chamber.	grs. CO_2 diffused at end of 6 hrs.	Total length of organ.
			cm.
Pneumatophore	10	·017	30·6
Horizontal root	10	·016	30
Pneumatophore	10	·007	26·5
Horizontal root	10	·018	30·3
Pneumatophore	10	·092	23·6
,, ...	10	·016	27·2
,, ...	10	·017	29·0
Horizontal root	10	·019	—
,, ,, ...	25	·064	—

cuticular interchange. Further experiments were made in order to determine the rates of gaseous diffusion in the horizontal roots and pneumatophores, the results being expressed on a six hour experimental period (Table III).

It will be seen that there is no significant difference between the rate of diffusion in the pneumatophores and the horizontal roots, even though the air spaces in the latter tend to be larger.

Absorption.—The pneumatophores of *Avicennia* arise from horizontal roots which are usually about 15–30 cm. below the soil surface, and which are commonly, though by no means always, in a permanent water table. The pneumatophores

pass vertically upwards from the horizontal roots, and they bear numerous functional lenticels in that portion which is above the soil surface. Passing downwards into the soil there are the anchoring roots, which arise on the ventral side of the horizontal roots. Spreading out from the pneumatophore at a depth of about 2–3 cm. below the soil surface there is usually a net of horizontal rootlets (fig. 1). Field observations suggested that as the soil height increased so new sets of



FIGS. 3 and 4.—3. The rooting system of *Avicennia nitida* under conditions of peat formation, $\times \frac{1}{4}$. 4. The same from among coral boulders, $\times \frac{1}{8}$.

absorbing rootlets developed higher up on the pneumatophores and the lower ones died off. In areas where there was evidence of rapid accretion the lateral rootlets were widely spaced on the pneumatophores (fig. 2), but in areas where there was little or no accretion one found a dense mat of rootlets all arising from about the same level (fig. 3). It was in such swamps that peat formation took place (Geograph. Journ.

XCV. 1940). This, then, is the normal structure of the underground system of *Avicennia*. On the fringes of the cays, however, the horizontal roots are frequently found growing along the soil surface amongst the blocks of coral, so that they are perpetually covered by the tide. Under these conditions the pneumatophores do not bear any lateral absorbing rootlets which grow out instead from the lower surface of the horizontal roots (fig. 4). There would thus appear to be definite evidence that under normal conditions the pneumatophores of *Avicennia* are responsible for bearing the lateral absorbing rootlets and that their development is controlled by the rate of accretion together with the position of the horizontal roots in relation to the soil surface.

Respiration.—It now remains to be considered whether the pneumatophores have any respiratory activity. The amount of carbon dioxide given out will be composed of two components, that due to any respiratory activity of the pneumatophores and that due to the respiratory activity of the horizontal roots. A modification of the apparatus employed by Troll and Dragendorff was used to determine the partial respiration (PR) which, over a period of two hours, ranged from ·03 to ·07 grs. carbon dioxide. The partial respiration is the component due to the pneumatophore. There is thus evidence that, under normal conditions, the pneumatophores are capable of carrying out some respiration, though the evidence obtained suggested that this was only a small proportion of the total respiration.

Summary.—A study of the functions of the pneumatophores of *Avicennia* leads to the conclusion that they are essentially the same as those described for the pneumatophores of *Sonneratia alba*, although there are certain minor differences. The pneumatophores function as

(1) Organs of gaseous interchange.

(2) Respiratory organs.

(3) Organs for bearing lateral rootlets and maintaining them at what appears to be the most suitable level.

Discussion.—

Professor R. R. GATES asked Dr. Chapman how the growth in length of the pneumatophores of *Avicennia* took place. Was there a meristematic zone?

A DISCUSSION ON PHYLOGENY AND TAXONOMY

ARRANGED AT THE REQUEST OF THE ASSOCIATION FOR THE STUDY OF SYSTEMATICS.

Mr. J. S. L. GILMOUR:—A study of the advance abstracts for today's symposium and of other current literature on the subject reveals, I think, three main views on the relationship between Phylogeny and Taxonomy. The first is that the aim of taxonomy is to classify living things according to their phylogenetic relationship. The second is that the aims of taxonomy and phylogeny are essentially distinct, but that ideally a taxonomic classification will, in fact, coincide with one based on relationship. The third view, while agreeing with the second as to the distinct aims of taxonomy and phylogeny, is sceptical as to whether a taxonomic arrangement can ever coincide exactly with one based on relationship.

Now it is essential, in considering these three views, to have a clear idea as to what is meant by the word relationship. The concept concerned is sometimes referred to as 'true relationship' or 'real relationship', and it is around this concept that the whole discussion revolves.

The first point to emphasize is, I think, that the criterion for assessing this 'true relationship' must, in the last analysis, be something distinct from an assessment of similarities and differences in attributes. For no biologist would hold that similarity in attributes is a *definition* of closeness of relationship, but rather that such similarity may *indicate* closeness of relationship, thereby implying that relationship is ultimately judged on some criterion which does not involve assessment of resemblance. In searching, then, for a definition of relationship, we must be careful to exclude any criterion which depends for its validity on assessing similarities and differences between organisms.

Bearing this in mind, let us examine the two main interpretations which can be given to the word relationship as used by taxonomists and phylogenists. These may be called the 'group concept' and the 'lineage concept' respectively. The 'group concept' interprets relationship as a relationship existing between taxonomic groups analogous to the genealogical relationship existing between individuals. This concept is expressed in the construction of phylogenetic trees, analogous to genealogical trees, the simplest unit of which is the origin of one group from another, analogous to the origin of a child from its parents. Consideration of such trees, however, reveals that their construction must involve inevitably the assessment of similarities and differences between organisms. For the basic fact which is represented by the origin of one group from another is that certain individuals gave rise to

certain other individuals, and it is clear that the decision as to the group in which the originating individuals should be placed is a taxonomic one, involving the assessment of similarities and differences. If one alters the taxonomy, one alters the phylogeny. This has been well summed up by Turrill in the phrase ' In order to construct group phylogenies, one must first make the groups '. In any interpretation of relationship on the group concept, then, we find ourselves arguing in a circle. We say, in effect, that similarities indicate relationship, and that relationship is based on similarities. It is, I think, clear, then, that the group concept of relationship does not give us that independent criterion of relationship that we are seeking.

If we turn to the lineage concept, however, we find quite a different state of affairs. This concept may be defined as follows :—The relationship between groups is an expression of the actual genealogical relationship of the individuals concerned. In other words, when we say that group A is more closely related to group B than to group C, we mean that the individuals of groups A and B are more closely related genealogically than are the individuals of groups A and C. Or, put in terms of lineages, the lineages which have gone to build up groups A and B are more closely related than the lineages making up groups A and C. Now the criteria for testing the closeness of genealogical relationship between individuals or lineages are something quite independent of any similarities or differences in their attributes. For example, two individuals which possess a common pair of grandparents are cousins whatever may be their attributes. I suggest, therefore, that if we are to seek a concept of relationship whose criterion is independent of taxonomic judgment, we must accept the lineage concept as the only one that makes sense.

Further examples of the differences between these two concepts are discussed fully in Bather's paper on ' Biological Classification, past and present ' (Quart. Journ. Geolog. Soc. LXXXIII, pt. 2, 1927).

Before considering the effect of the acceptance of this definition of relationship on the connexion between taxonomy and phylogeny, let us examine for a moment its effect on the concept of phylogeny itself. If relationship is really genealogical relationship—is phylogeny, then, nothing but genealogy ? I do not not think any biologist would accept this view. I suggest that phylogeny may be defined as ' the history of the origin and development of taxonomic groups '. Now, thus defined, phylogeny is clearly not a simple concept. At least the following separate factors must be taken into consideration when reconstructing the history of a taxonomic group :— Firstly, the geographical area or areas where the group first

appeared ; secondly, the period or periods of time when it first appeared ; thirdly, the characters of the individuals from which it evolved ; fourthly, the number of lineages which went to form it and the relationship between them ; and finally, the subsequently evolution of the group. All these factors are, of course, interconnected, but they are essentially distinct, and should not be confused. Recently this multiple character of phylogeny has received considerable attention, notably from Professor Lam of Leiden (see Acta Biotheor. II, pt. 3, 1936), and terms have been suggested to express the different factors, such as polytopic, polychronic, polyrheithric and multilineal.

If this picture of phylogeny be accepted, together with the lineage concept of relationship, then it is clear that relationship is only one of several factors which together make up the phylogeny of a group. If, therefore, one constructs a classification purporting to be based on ' true relationship ' (that is, on lineages), it is misleading to label such a classification as phylogenetic, since only one of the phylogenetic factors is being considered. It is, I suggest, preferable to call such classifications ' lineage classifications ', as this indicates clearly the basis on which they are made ; and this is, in fact, done explicitly or implicitly by many palaeontologists. If it is desired to express what may be called the ' total phylogeny ' of a group—that is, to express all the factors involved—surely the only method is to construct a series of diagrams, each designed to exhibit a particular factor or factors. Here again, Professor Lam (loc. cit.) has recently discussed the principles on which such diagrams should be constructed.

To sum up our conclusions so far, we may say that classifications based on so-called ' true relationship ' must be regarded as lineage classifications, and that, as lineage is only one of several factors involved in phylogeny, it is misleading to call such classifications phylogenetic, or based on phylogeny.

The next question is, what is the relation between such ' lineage classifications ' and taxonomy ; in other words, what is the effect of the acceptance of the lineage interpretation of relationship on the three views mentioned in my opening remarks ?

The first point I want to make is that taxonomy has definite and clear-cut methods and aims of its own, quite apart from any connexion that there may be between a taxonomic and a lineage classification. And I think this is what one would expect when one considers that a natural classification was carried out some time before phylogenetic ideas were introduced by the acceptance of evolution.

What are these methods and aims ?

Classification in general, both of animate and inanimate objects, consists in grouping together individuals which have certain attributes in common. The groups or classes thus formed are then used for making inductive generalizations. Thus, one groups together, say, individual books into classes according to their subject matter, and again according to their date of publication, and, by comparing the resulting classes, one can make the inductive generalization, say, that more detective stories were published in the twentieth than in the nineteenth century. Thus, classification is not an end in itself, but is a means to an end, namely, the making of these inductive generalizations, which are the subject matter of science.

Now, it is clear that the particular attributes selected as the basis of any classification depend on the purpose in making the classification. Thus, in the example quoted, the classifier, before making his classification of books, had in mind the purpose of investigating the relationship between subject matter and date of publication, and selected his attributes accordingly. This characteristic of classification, namely, the fact that the attributes chosen as a basis depend on the purpose of the classifier, is of great importance in considering the aims and methods of biological classification.

Bearing this in mind, we must now distinguish between two types of classification, often called natural and artificial, though, as I shall explain later, these terms are rather misleading. Broadly speaking, a so-called artificial classification is one based on a limited number of attributes, made for the specific purpose of establishing the relationship between these attributes and others. The example quoted regarding books is an artificial classification in this sense, since certain attributes were deliberately selected as a basis. So-called 'natural classifications', on the other hand, are based, not on a few specially selected attributes, but, so far as possible, on general resemblance between individuals, taking into consideration as many correlated attributes as possible. The purpose of making such classification is twofold, as was clearly pointed out by T. H. Huxley, namely, firstly, to epitomize, simply and conveniently, those empirically discovered correlations on which the classification is based, and thus make them more available for use; and secondly, to enable predictions to be made about individuals subsequently discovered. Thus, the creation of the family Malvaceae is, in effect, a convenient summary of the fact that the attributes on which it is based have been found empirically to be correlated together, and the act of expressing these correlations under a single group name enables us to refer to them conveniently and to use them for further correlations and generalizations. Also, having thus

drawn attention to and epitomized those correlations, we are enabled to predict that any individual which is found to possess certain of these attributes probably possesses also certain others correlated with them. For example, if we find a plant whose morphological characters lead us to place it in the Malvaceae it will probably be found to possess a mucilaginous sap and so on.

I suggest, therefore, that a natural classification in this sense has perfectly legitimate aims of its own which were recognized more or less clearly by the pre-Darwinian taxonomists, and that, whatever the relationship of this type of classification to phylogeny or lineages may be, these aims should be kept clearly in mind.

Finally, having attempted to define what is meant both by relationship and by a natural classification, we are in a position to discuss briefly what is the connexion between them and to try and decide between the alternatives mentioned at the beginning of this contribution.

In the first place, I think it is clear that a lineage classification will not necessarily coincide with a natural classification as defined above. To take a very simple example, we know, both by observation and by genetical experiment, that two cousins may be more alike than two brothers. I suggest that the true position is, not that general resemblance is a *measure* of relationship, but that relationship is, in part, an *explanation* of general resemblance. This point of view has recently been forcibly put by Bremekamp in an article in ' Chronica Botanica ' (v, p. 398 ; 1939). An analogy from the non-living world will perhaps show what I mean. If one attempts to make a natural classification of motor cars built between 1895 and 1940, the resulting classification would probably correspond roughly to date of manufacture rather than to make of car, because two makes of 1895 would have more attributes in common than two cars of the same make of 1895 and 1940. On the other hand—and this is the important point—the classification would not coincide exactly with one based on date of manufacture. Other factors, besides date, contribute towards causing similarity of attributes—for example, one make might remain unchanged for many years, and this would upset an exact correlation. In other words, one can say that the influence of date of manufacture on attributes is one of the prime factors in making a natural classification of cars possible, but that similarity of attributes is not an exact measure of date of manufacture. Applying this analogy to living things, one can say that while closeness of relationship is one of the most important factors causing similarity of attributes, such similarity is not an exact measure of relationship. Here, again, other factors, such as convergent evolution

due to parallel mutations or similarity of environment, upset an exact correlation. I suggest, then, that the correct way of expressing the connexion between relationship and a natural classification is to say that relationship is one of the most important factors in making a natural classification possible, but that natural groups and groups based on relationship do not necessarily coincide.

This does not mean, of course, that a classification which is, in fact, based on relationship has not a useful and legitimate place in biological classification; but it should be regarded as distinct in aims from a natural classification. It is, in fact, an artificial classification in the sense defined earlier, since it is a classification based on a specially selected attribute, namely, relationship. As I said, however, the terms artificial and natural, as applied to classifications, are ambiguous and misleading, and it would seem to be preferable to use the terms 'general classifications' for those based on a consideration of general resemblance and 'special classifications' for those based on selected attributes for special purposes. Lineage classifications would thus be special classifications constructed for the purpose of comparing relationship with other attributes.

There are two final points that I would like to touch on.

Firstly, it may be said that taxonomists, when making their classifications, do not in fact consider all attributes as of equal value in assessing resemblance and difference, but that they weight certain attributes which have phylogenetic significance, and thus the resulting classification can be said to be phylogenetic. In considering this point we must distinguish between two methods of weighting characters. The most usual method, I think, is as follows. A taxonomist first groups his individuals according to general resemblance, considering, as far as possible, all attributes, and he then examines the resulting groups and finds empirically that certain characters are more important than others in the sense that they have a larger number of other characters correlated with them. It is by this method that such characters as angiospermy and gymnospermy, monocotyledony and dicotyledony had been found to be important, long before the acceptance of evolution. These characters, once discovered by this method, are then weighted in making subsequent general classifications. Any phylogenetic significance that they may be given is, as it were, an afterthought, attached to them after they have been discovered by empirical observation. And the reason that it is felt necessary to attach this significance is, I suggest, the lack of realization that a general classification has an aim of its own. It is felt that unless a classification can be shown to be phylogenetic it has no validity or *raison d'être*, which, as I have tried to show, is far from being the case.

There may, however, be another method of weighting characters. A taxonomist may say that he will definitely select as important those characters which are least likely to be influenced by the environment, and are thus most likely to show true relationship. If he does this, it is clear that the resulting classification will be a special classification based, so far as the premises are sound, on relationship, and, while perfectly valid for its own purpose, must not be confused with a general classification as defined above. In fact I think the majority of taxonomists use the first method of weighting characters. It is interesting to note, for example, that Mr. Lack, at a meeting of the Ecological Society held last week, made the statement that the characters separating genera in birds were largely adaptive characters.

The second point is as follows. It may be objected that this attempt to clarify the aims of taxonomy is really a waste of time, that it doesn't matter what a taxonomist's aims are—the results will be much the same, anyway. I think, however, that anyone who has studied the various attempts in recent years to solve the problem of incorporating modern data from genetics, cytology and ecology into taxonomic categories, or the discussions of the palaeontologists on the best methods of reconciling lineage and character classifications of fossil material, will agree that one of the main difficulties is just this problem of what exactly taxonomists are aiming at in classifying living things.

Mr. O. W. Richards :—Granted that the existing animal kingdom has arisen by a process of continuous evolution, a 'phylogenetic classification' must exist. It could be exhibited, for instance, by arranging on a large table all the specimens of all species that have ever existed. To some extent the classification based on such a collection would exhibit an anastomosis of separate lines owing to the polyphyletic origin of some species or genera, but it is almost certain that in the main it would be of the classical tree-like form.

On the other hand, the absence of almost all palaeontological data does not make it impossible to arrive at a useful classification. The material can be made to fall into groups sharing a progressively greater number of characters. Moreover, it is usually found that though more than one method of arrangement could be adopted (by making different characters the index of primary divisions), one scheme is evidently the best—that is, it leads to an arrangement in which a higher number and a more varied assortment of characters is correlated. The problem under discussion is how far the 'useful classification' of the present paragraph is the same as the 'phylogenetic classification' of the first.

It is surprising how little the methods of the pre-evolutionary taxonomists differed from those of modern workers. They were, of course, familiar with only a fraction of the morphological characters which are known today, but by adopting dichotomic systems they were inevitably led to build up taxonomic units defined by groups of correlated characters. Many of their units broadly correspond to groups still recognized at the present day.

It is important, then, to consider how far the acceptance of the evolution theory has modified the work of taxonomists. It has been suggested that a useful and thoroughly workable classification can be constructed without assuming any theory of evolution. Nevertheless, I believe evolutionary theory has had a profound influence on post-Darwinian taxonomy. This influence has been felt, perhaps, in two main ways :—

(1) Where by an organ a number of species or genera can be arranged serially, showing progressive change, this is generally thought of as having *some* relation to an evolutionary series. This will almost certainly affect the way the series is treated by taxonomists.

(2) Our general knowledge of the course of evolution and of the habits of animals leads us to regard changes as more likely to occur in some directions than in others. Such knowledge is used to orientate series of the sort just referred to.

Perhaps two examples, one from the Diptera and the other from the bees, will illustrate what I mean.

A number of wingless species are known as the flies of the family Sphaeroceridae. When they lose their wings, the thorax becomes considerably modified, the abdomen enlarged and the bristles often reduced, so that a recognizable facies is produced. This has been given a generic name, *Aptilotus* Mik., to which several species have been assigned. Recently, more wingless forms have been discovered, and if these were all placed in that genus a group would be formed which (on phylogenetic grounds) has a most unnatural distribution. By giving greater weight to certain other characters, the wingless species can be assigned to a number of groups, each confined to a restricted region. In several cases the winged stock from which these groups arose can be suggested. This classification certainly more nearly expresses the phylogeny of the group, and is probably also more useful.

Amongst the bees there is a number of cuckoo genera, of which the larvae live as parasites in the nests of industrious species. These cuckoo bees have evolved from industrious species, and in favourable examples the resemblance is still so close that the ancestral genus is pretty certain. Yet some of the genera no longer closely resemble any industrious genus. Moreover, there is a very definite ' parasitic facies ',

dependent not only on the loss of pollen-collecting apparatus, but on the presence of bright, sometimes wasp-like colours, etc.; most parasitic bees can be recognized as such without observation of their habits. For these reasons two different classifications have grown up. One endeavours to place each parasitic genus next to its supposed ancestor. This is the phylogenetic scheme, and in general, I believe, the best one; but it has the disadvantage that a number of genera are hard to place. The other scheme places all the parasitic bees together in one group, which, at least in the female sex, is easily defined by the absence of pollen-collecting apparatus. Sub-groups within this assemblage roughly correspond to the various lines of ancestry. Although artificial, this scheme has certain advantages in classifying the bees of, say, Africa, which are very imperfectly known.

But apart from whether our classifications are actually correlated with phylogeny, it is sometimes suggested that it would in any case be better if they were not. A clear-cut 'logical classification' implying no theory is, it is said, the most useful. I think it is too easy to overlook how often phylogenetic implications must creep in unawares. For instance, any consideration of geographical distribution automatically includes the idea of evolution on different land masses. Similarly, it is frequently necessary to decide which of two characters shall be regarded as primary in classification. Judgment is often influenced not merely by the sizes of the correlated groups of characters which result from the alternative schemes, but also by ideas as to the biological significance of the characters. Even when we draw on characters from different parts of a life-history, I think we are often committed to some evolutionary assumption.

Although for many practical purposes it is the clear definition of genera and species that matters, rather than the arrangement of the families, yet a rearrangement of genera not rarely leads to the search for and the discovery of new characters, one of the most important activities of a taxonomist. Moreover, in the long run I feel sure that a classification approximating as nearly as possible to phylogeny will be practically the most successful. No doubt much of our classification is likely to be a defective guide to phylogeny and, what is perhaps more important, *we have no independent means of judging how defective*, if fossils are lacking. Moreover, it is very easy to overestimate the value of classifications based on merely *morphological* characters as indicators of phylogeny, though this does not necessarily detract very seriously from the value of the classification for other purposes.

Yet if we believe in evolution let us take it seriously. Though we should never let evolutionary theory interfere

with a key intended for the identification of specimens, we should also never allow the needs of identification to spoil the text.

Dr. T. A. Sprague :—I will not attempt to follow the first speaker into the highly abstract field which he has chosen as his own, but will try instead to give the views of a practical taxonomist. Before doing so, I should like to suggest, however, that he has confused the issue by using the expression ' natural classification ' in a sense different from that in which it is usually employed by taxonomic botanists. He defines it as a classification in which those individuals which have the greatest number of attributes in common are grouped together. He then proceeds to argue that such a classification does not necessarily coincide with a phylogenetic one. I agree ; but neither does his so-called natural classification in logic coincide with what is generally termed natural classification by taxonomic botanists. Hence his arguments do not prove that the latter is not phylogenetic.

I have four points to make :—(1) that a natural classification in taxonomic botany does not *necessarily* coincide with a natural classification in logic ; (2) that the so-called natural classification in botany has been developed synthetically, by a process of trial and error, and is not based on arbitrary selection of characters ; (3) that there is reason to believe that the so-called natural classification of the Angiospermae is approximately natural in the phylogenetic sense, so far as the groups themselves are concerned ; and (4) that, in the absence of relevant fossil evidence, the phylogeny of the orders of Angiospermae is at present purely speculative.

1. The idea that a natural classification in botany coincides with a classification based on maximum agreement in total characters is rather widespread. Asa Gray (' Structural Botany ', ed. 6, 1879, p. 331) stated that ' a natural classification in botany aims to arrange all known plants into groups in a series of grades according to their resemblances, and their degrees of resemblance, in all respects, so that each species, genus, tribe, order, etc., shall stand next to those which it most resembles in all respects, or rather in the whole plan of structure. For two plants may be very much alike in their external appearance, yet very different in their principal structure '. Here the words ' in the whole plan of structure ' are significant. Agreement in general plan may outweigh agreement in details.

It may perhaps be true that the individuals composing a species show greater resemblances among themselves than with individuals belonging to other species : but can this be proved ? First, what characters should be taken as units in estimating

the amount of agreement in total characters? The general shape of a leaf, e.g. ovate, lanceolate, etc., is commonly treated in technical descriptions as a single character; but a little consideration will show that it is a complex of characters, including ratio of length to breadth, position of maximum breadth, rates of tapering to base and apex, etc. Secondly, it is virtually impossible in the higher plants to take all resemblances into consideration. According to Moll ('Phytography as a Fine Art', 1934, p. 484), 'a complete pen-portrait of a higher plant will easily take a man's work during a whole year'. Hence the most that can be done is to take into consideration such characters as experience has shown to be useful in classification, together with any additional ones that may be observed.

There is less reason to believe that all the species of a large genus show greater resemblances in total characters among themselves than with species belonging to related large genera. Many specific characters are adaptive, and parallel adaptations to particular climatic or edaphic conditions are found in different genera (cf. Watkins, 'Stem Anatomy of Chaparral Shrubs', in Bot. Gaz. CI, 1939, pp. 391–402). It is possible that, owing to the occurrence of such parallel adaptations, individual species (or groups of species) in one genus may show greater resemblances in total characters with species of a related genus than with others of their own genus. In related families there is an increased probability of the occurrence of such greater agreement in total characters between subordinate groups of one family and subordinate groups of the other.

It should be borne in mind that on the whole the number of *constant* characters of taxonomic groups tends to decrease as the rank of the group becomes higher. All characters that are constant in a family are, *ipso facto*, constant in all its subordinate groups. But in a species of a given genus such of the constant characters as are diagnostic, are, *ipso facto*, not constant in that genus. The higher the rank of a group, the greater the difficulty of defining it, owing to the smaller number of constant characters. The constant characters of a large family are fewer than those of its individual genera, and those of an order comprising several families are fewer still. In these groups of higher rank the general plan of structure becomes more important, e.g. the scorpioid cyme of the Boraginaceae and the sympodial stem of the Vitaceae. Admittedly, in assessing degrees of resemblance, the general plan is the equivalent of several or many special characters. But what arithmetical value should be placed on it? In the light of the preceding considerations the view that a natural classification of living things consists, in practice, of grouping together those individuals which have the greatest number

of attributes in common seems an over-simplification of the position.

2. The so-called natural system of classification in the Angiospermae has been built up, first by the recognition of species, then by grouping these into genera, and then the genera in their turn into families. The first recognition of species long antedates civilization. Many savage tribes have an intimate acquaintance with a large number of species, based on their general appearance, properties and uses. A professional taxonomist of today, beginning the study of a genus in a herbarium, will spread out all the material available and endeavour to sort it into groups according to facies. Facies may be defined as the general effect produced on the eye by the sum total of all the visible external characters. A preliminary sorting of plants into different groups by means of facies is certainly not based on arbitrary selection of characters, though it may be based on subconscious abstraction. The distinguishing characters (if any) of the groups obtained by this method are then observed, and the groups are then modified, if necessary, according to the incidence of the characters noted. Finally, a number of more or less equivalent groups called species are recognized.

Historically, the next step in the evolution of the natural classification of Angiospermae was the grouping of species into genera. This also was effected by a process of trial and error, resembling the gradual piecing-together of a jigsaw puzzle, many of the parts of which are missing. Again the process was one of synthesis, checked by analysis of the characters of the resulting groups. Finally, the genera were grouped into families on the same basis. In all this, the existence of what have been called chains of related groups, i.e. of groups the successive members of which differ relatively little from one another, has naturally been of great asssistance. At all stages of progress certain types of character have been found to distinguish the groups previously recognized, and these characters have accordingly been utilized as a guide in the tentative construction of new groups of the same rank. This is not arbitrary selection of characters.

3. Do the so-called natural groups of plants now recognized correspond on the whole to the final branches or twigs of the phylogenetic tree ? It is perhaps significant that those who have spent their lives in the study and improvement of the natural system should be convinced that it corresponds to something real in nature, and that they are, in fact, not inventors but discoverers of parts of the natural system. The group called Malvaceae was discovered, not made, by taxonomists.

The basis of the taxonomists' belief lies in the gradual, continuous and never-ending improvement of the natural

system from the sixteenth century onwards, and still more in the repeated confirmation of many parts of that system. The number of characters taken into consideration is a mere fraction of the whole, and the system has been built up largely on external morphology. If the resulting natural classification in botany were merely, as has been argued, a particular example of the so-called natural classification in logic, why should characters previously unknown and unconsidered so frequently prove to be correlated in the same way? If, on the other hand, the groups previously recognized are monophyletic, there is every reason to expect such correlation. Hundreds of examples might be given of groups, based solely on examination of their external morphology, which have been confirmed later on by investigation of anatomical, cytological and biochemical characters.

Cucurbitaceae was recognized as a family long before it was discovered that all its members possessed bicollateral vascular bundles, and Polygalaceae long before it was known to be characterized by a highly peculiar type of pollen-grain. The tribe Eragrosteae was first recognized as a distinct group on consideration of its external morphological characters: subsequent examination of the anatomy and cytology yielded five additional diagnostic characters (Sprague, 'Taxonomic Botany, with special reference to the Angiosperms', in Huxley, 'The New Systematics', 1940, p. 442).

The families Campanulaceae, Goodeniaceae and Stylidiaceae have long been placed near the Compositae: it is now known that they also produce inulin in place of starch.

The order Centrospermae has long been recognized as a highly natural group, and the order Opuntiales (Cactales) has been considered by many taxonomists to be most nearly related to Centrospermae. According to recent investigation, nitrogenous anthocyanins have been discovered in 25 species (Lawrence, 'The Distribution of Anthocyanins in Flowers, Fruits and Leaves', in Phil. Trans. Roy. Soc. Lond., ser. B, no. 567, ccxxx, 1939, p. 176). It is perhaps significant that 20 of these belong to the Centrospermae, 4 to the Opuntiales, and only one to a species of another order.

It has been suggested that the agreement in characters found in apparently natural groups may be due not to common descent but to convergence, and that many of these groups are polyphyletic, i.e. that they have originated from two or more groups of the same rank. Certain biological progressions seem to have taken place independently in numerous lines of descent. In connexion with pollination by insects, it is highly probable that reduction in the number of stamens and a change in floral symmetry from actinomorphy to zygomorphy has occurred in many phyletic groups. In connexion

with seed-dispersal, it is noteworthy that most annuals have dry fruits, and this may perhaps be regarded as an adaptive character in annuals. Similarly, certain anatomical characters have been developed in connexion with special climatic or edaphic conditions.

It may be agreed that the possession in common of several such adaptive characters does not necessarily indicate common descent (Wernham, 'Floral Evolution, with particular reference to the Sympetalous Dicotyledons': IX, in 'New Phytologist', XI, 1912, pp. 393–4), though such descent becomes increasingly more probable the greater the number of unconnected adaptive characters concerned. The existence of a large number of coincidences generally points to an underlying common cause.

The probability of a particular group being monophyletic is greatly increased when its members have several apparently non-adaptive characters in common. Such characters have been termed 'fortuitous' (Wernham, loc. cit. p. 392).

The family Polygalaceae is generally regarded as a very 'natural' one. In addition to numerous adaptive characters, it has a series of fortuitous ones. The inflorescence is purely racemose (i.e. indefinite), the general plan of the flower, as shown in a floral diagram, shows only slight modifications, the sculpturing of the pollen-grain is highly characteristic, and the wood-anatomy of all the woody genera and species is very similar. Furthermore, a highly peculiar type of anther-dehiscence occurs in several genera, and a peculiar type of nectary occurs in an unusual position (on the bracts) in several genera. Such cumulative evidence seems overwhelming. Can any hypothesis, save that of common descent, explain the facts?

4. Most of the families of Angiospermae have been established by synthetic methods, and are generally regarded as probably monophyletic. The same applies to the classes Dicotyledoneae and Monocotyledoneae. On the other hand, many of the groups intermediate in rank between the families and classes have been established by analytical methods and appear to be polyphyletic. In the Dicotyledoneae only about one-third of the orders seems to be well-founded. The phylogenetic relationships of even these orders are at present highly speculative.

So-called phylogenetic trees of the orders of Angiospermae appear on examination to be based on two assumptions: (1) that certain evolutionary progressions, chiefly floral ones, have taken place; (2) that those groups characterized by most of the supposedly primitive floral characters in these progressions were necessarily the stock from which the groups with more advanced floral characters were derived. Wettstein,

(' Handbuch der systematischen Botanik ', ed. 4, 1935, p. 1068) based his phylogenetic tree of the Angiospermae on various evolutionary progressions, postulated by him, including gymnospermy→angiospermy, unisexual flowers→bisexual, apetaly→polypetaly→gamopetaly, polymery→oligomery, apocarpy→syncarpy. Similar assumptions underlie the diagram of inter-relationships of the Angiospermae given by Pulle (' Compendium van de terminologie, nomenclatuur en systematiek der zaadplanten ', 1938, after p. 338). Hutchinson (' The Families of Flowering Plants.—I. Dicotyledons ', 1926, diagram after p. 8) postulated a different set of evolutionary progressions. What the diagrams purport to represent in each case is the phylogenetic relationship of the orders concerned. What they actually seem to represent is a series of stages in the evolution of the flower, according to the particular author's postulates, that is, they are morphogenetic diagrams. The authors place at the beginning of their diagram the orders which are at an early stage in most of the progressions postulated, and at the end those which are at a late stage in most of the progressions. They assume that because the former exhibit relatively primitive characters *as far as the selected progressions are concerned*, they have necessarily given rise to the latter. It may be pointed out that the characters taken into consideration represent a mere fraction of the whole, and that the progressions themselves are essentially adaptive. Hence the greater the probability that a particular progression has occurred, the greater will be the probability that it has occurred independently in several or many phylogenetic branches. To illustrate these points, a small piece of Hutchinson's diagram may be considered. The *Ranales* occur at the bottom of one of the two trees, apparently because they are mainly bisexual, partly hemicyclic, hypogynous, generally petaliferous, polystemonous and apocarpous, and because they are mostly perennials. The *Saxifragales* are shown as arising from the *Ranales*, apparently because they are considered by the author to be phylogenetically related to the *Ranales*, and because they represent a later stage in his selected progressions. Similarly, the *Caryophyllales* are derived from the *Saxifragales*. No reasons, however, are given in support of such assumed phylogenetic relationships. Phylogenetic diagrams should be accompanied by a detailed analysis of all the available characters and tendencies of the groups with which they are concerned. Otherwise they must be treated merely as an expression of personal views unsupported by the production of evidence.

Dr. E. I. White :—In discussing the desirability of using phylogeny as the basis of taxonomy it is obviously essential

that the meanings of these two terms are quite clearly understood. Primarily taxonomy and the study of phylogeny are distinct and not necessarily interrelated. The former deals with the arrangement of organisms into groups for convenience of study, the contents of the groups being determined by the number and by the nature of common characters, which may be arbitrary. There are no limiting factors to the nature of the groups other than those due to the particular purpose for which the classification is used—the term 'taxonomy' in no way implies a 'natural' classification, whatever that may mean, nor need taxonomy be based on phylogeny. Indeed, the early essays on taxonomic arrangement, such as that of Linnaeus, were, as your President has recently reminded you (J. Ramsbottom, Pres. Address Linn. Soc. Lond., Sess. 1937–38, pp. 197 etc.), entirely without any idea of evolutionary principle, but they were, none the less, examples of true taxonomic work, and for the time the best of their kind. Classifications based on colour or shape may be perfectly good examples of taxonomy if suited to their purpose, but we are here concerned with the general taxonomy used by working systematists whose aim is not only to make a convenient systematic arrangement for purposes of identification, but also one that attempts to show the affinities of the animals or plants under consideration. And this brings us to phylogeny, which is concerned only with the ancestry of organisms, that is to say, their true relationships, which have to be deduced by the careful appraisement of characters common to the several organisms, but whose selection, although naturally subject to the vagaries of human judgment, cannot be arbitrary. To most palaeontologists, who, by reason of the nature of their work, must always consider the time-factor, a classification without a phylogenetic implication seems pointless. As is well enough known, the study of stratigraphy shows that horizons in the succession of strata are characterized by the level of development of the faunas (or floras), that is to say, of the component organisms; and the relationships of similar genera and of various species of a genus at different horizons are cardinal points of study—to ignore them would deprive palaeontology of one of its primary uses. Naturally, by reason of the all too familiar imperfection of the geological record, there are often great difficulties in determining relationships, or convergent evolution may further obscure them *. But these difficulties are only to be considered as temporary and do but add zest to our studies. We, of course, appreciate the difficulties

* For a fair exposition of the palaeontological viewpoint, see Arkell & Moy-Thomas, 1940, 'The New Systematics', Oxford, p. 395.

of workers on certain recent groups, both in Botany and Zoology, where fossil evidence may be extremely meagre; yet it came as a surprise to discover that there were workers in the field of systematics who regarded the use of phylogeny as a basis of classification as a definitely false step, not only in their own groups, but apparently in others where evidence of phylogeny may be ample.

It is not so much the practice of using non-phylogenetic taxonomy (for which there may at the time be no alternative) that is to be deplored, but the attitude of mind that accepts this position and is content to adopt a classification based on ignorance rather than consciously seek to work out one based on knowledge—for this is a policy of despair. Indeed, it is difficult to understand the aims of taxonomists who ignore phylogeny. Is their object merely to pigeon-hole material? Many at any rate seem to aim no higher.

To sum up, we may say that, should all the facts be known, a phylogenetic tree and a sound taxonomic arrangement would coincide, but this postulates evidence both in space and time. It is the work of the palaeontologists to provide such evidence, and to them a taxonomic arrangement without a phylogenetic basis is only a temporary expedient due to lack of evidence. To think otherwise is to deprive systematic work of the one factor that gives it vitality and elevates it to the dignity of a science.

Dr. H. Hamshaw Thomas, in a written communication which was read for him, stated that botanists have shown an inclination to discard the dictum that taxonomy and phylogeny are intimately connected, although there has been latterly much research which bears on both. He suggested that illogical morphological concepts have brought this about. He added that though the Caytoniales are not necessarily ancestors of the Angiosperms, they show that a closed ovary may have originated from a structure very different from an inrolled or peltate leaf. With long-inherited far-reaching generalizations deductively made, but now weakened by inductive reasoning, every phylogenetic speculation and much of angiosperm taxonomy has been reduced to a mass of ruins; and at the moment phylogeny has nothing to give to the taxonomist save pure guesses.

He asked for a critical and ruthless examination of the history and logic of current ideas and generalizations, for the newer investigations now being carried out by a few investigators will lead to conclusions very different from those to which we have been accustomed, and far more trustworthy. Generalizations which remain unchanged for long periods of time should be suspect, while a steady series of modifications to our

general conclusions will usually indicate that the subject is being logically developed. Nevertheless, taxonomy, having its practical aspects, cannot and should not wait for the solution of evolutionary problems ; and in the meantime we are likely to achieve the best results by allowing taxonomy and phylogeny to develop independently.

Dr. Julian S. Huxley :—The believers both in a completely logical and in a completely phylogenetic taxonomy would appear to be aiming at ideals which are quite unattainable in practice ; in addition, both systems are in some cases not consonant with fact. For instance, taxonomic practice, at any rate in larger groups among animals, appears to base itself on the co-ordination of characters in an organizational plan, rather than on the totality of attributes ; and a phylogenetic classification simply will not fit cases such as reticulate evolution.

In general, however, the two concepts largely coincide. They coincide because the processes of mutation and selection distribute characters among taxonomic groups in such a way as to fulfil approximately the postulate of a maximum correlation of attributes demanded by the upholders of a logical classification. The more characters are available, the greater in general will be the approximation. Geographical distribution and palaeontological history are to be included among characters in this sense. In fossil material, however (e.g. molluscan shells), the number of characters may be very much limited compared with the range available to the student of living forms ; it is probably this which accounts for many of the cases of apparent parallel evolution to be found in the palaeontology of, e.g., Molluscs and Brachiopods.

When divergent groups have evolved separately for long periods, the co-ordination of character-distribution with taxonomic grouping will be very close. It need not be so close, however, when the divergence is of recent date ; in this case the chance of parallel mutations upsetting the co-ordination is much greater.

In one respect taxonomy would appear definitely to have a phylogenetic basis, in that named categories are in general monophyletic groups. Wherever the distribution of characters contradicts the hypothesis of monophyly for a group, the taxonomy demands revision : here the phylogenetic outlook can play a constructive part in taxonomy. This generalization may break down in regard to lower categories such as species, which in, e.g., apomictic and in reticulate evolution must be delimited purely on the basis of convenience. It also breaks down in the case of ' horizontal groups ' (e.g. genera) in palaeontology, which may be merely stages

run through independently by several lineages, and yet necessary categories for the sake of taxonomic convenience. But in regard to higher categories the principle certainly holds.

When it comes to detailed taxonomic *arrangement*, however, as opposed to taxonomic naming, it is difficult to see how a phylogenetic basis can be found for this. As speakers today have shown, the elaborate trees and other diagrams of arrangement (relationship) proposed, e.g. for the groups of higher plants, are largely contradictory *inter se*, and must be regarded as highly speculative. Whenever there is reasonable certainty as to arrangement—e.g. when one set of families or orders can be deduced to have a common origin separate from that of others—this can, and should, be represented by means of named categories, such as superfamily, suborder, subclass, etc. Where this is not possible, the arrangement (e.g. the order in which groups of a certain taxonomic category are enumerated) should not be presumed to have any phylogenetic meaning.

Even if we had a full knowledge of the phylogeny of, say, all genera and families within an order, the diagrammatic representation of this would be exceedingly complex, and must be held to be a ' subsidiary classification ' in Turrill's sense (Experimental and Synthetic Plant Taxonomy, in ' The New Systematics ', Oxford, 1940, p. 46) rather than falling within the province of taxonomy *sensu stricto* (Turrill's ' alpha or orthodox taxonomy ').

Gilmour referred to the fact that taxonomic practice was actually little altered by the introduction of the idea of evolution and phylogeny into biology. We must remember, however, that the more philosophically-minded pre-Darwinian taxonomists thought in terms of an ' ideal plan ' or archetype which was modified in detail in various sub-groups of a major group (see, e.g., T. H. Huxley on the major classification of the Mollusca, in Phil. Trans. Roy. Soc. CXLIII, 1853, p. 29), and that this is in point of fact a symbolic representation of phylogeny.

Thus, while taxonomic practice inevitably rests upon the evaluation of characters, and while phylogenetic relationship must always (in the absence of full palaeontological data) remain a deduction, the phylogenetic idea, whether directly, or symbolically in the form of a modifiable archetype, may, and often does, aid the taxonomist in evaluating his characters and in framing his categories.

Dr. W. B. TURRILL said that in his view most phylogenetic schemes proposed for the Angiosperms were a mixture of fact and speculative fiction.

There was an important but subtle danger in making and

using such schemes : that a scheme was made on the basis of supposed phylogeny and then was used later as a proof of the truth of the supposed phylogeny. When all camouflage was removed many phylogenetic arguments were found to run in a circle—that a group was primitive because its members had primitive characters, while the characters were primitive because they appeared in a primitive group.

Professor Sir WILLIAM WRIGHT SMITH pointed out that the problem which confronted the botanist in attempting the interpretation of the past was more difficult than what faced the zoologist. The fossil record, very imperfect though it was, did present to the zoologist some guidance in interpreting the history of the past ; but when it came, for example, to searching for the origins of the Angiosperms, the data were meagre in the extreme. We know practically nothing about the origin of the Angiosperms. Our data are the data of the present day. As soon as we attempt to take a few steps backwards we are at once in the realm of speculation. The speaker confessed that most interpretations of the past history of the Angiosperms reminded him strongly of the many prophets who had endeavoured to give a picture of the conditions which might prevail in a future world. Such prophets were numerous, and out of every hundred it follows that ninety-nine will be wrong, and there is no guarantee that the hundredth is any more worthy of credence. Dr. Sprague had put on the screen samples of these phyletic interpretations from different authors. Divergences of opinion were many and often fundamental, and it is doubtful whether many botanists believed in any one of these genealogies. If a family or a genus was submitted in turn and independently to a geographer, to a cytologist, to a geneticist, to a botanist and to a horticulturist, it would be surprising indeed if the pictures drawn up by these five showed any general harmony. In cases, however, where consultation among the five was carried out, there would no doubt be some measure of agreement as regards the arrangement of the units as they stand at the present day ; but it would not be wise to anticipate agreement once each of them began to tell the story of the evolutionary past. There is no reason why such attempts should not be made, as they serve as illustrations of possible relationships ; but as far as the botanical past is concerned the conclusions arrived at can only be deemed guesses, more or less splendid, but in the nature of things soon to be overturned as further information becomes very slowly available.

Dr. R. MELVILLE said that it was clear from the variety of opinions expressed that afternoon that a wider understanding

of the philosophical basis of classification was desirable. Mr. Gilmour had given a lead in the right direction with his lucid exposition of the subject. It was evident from the remarks of several speakers that their aim was to produce a phylogenetic classification based only on lineages. This was a narrower conception of a phylogenetic classification than that defined by Gilmour, and must be regarded as a special classification the main aim of which was to express the evolutionary development of the groups being studied. Such an approach was natural for the palaeontologist on account of the nature of the evidence with which he was dealing. To a lesser extent this was true for the zoologist, who had a considerable volume of evidence from palaeontology, but the position was very different for the botanist. Present botanical classification was a kind of hybrid between a ' logical-natural ' and a phylogenetic classification. Further progress would follow from a clearer apprehension of the purpose of special classifications and their philosophical basis. It had been asked : what is the use of the ' logical-natural ' classification ? Whereas the aim of the phylogenetic classification is to epitomize evolutionary history, the ' logical-natural ' classification by attempting to correlate all attributes of living organisms has wider application, and is probably the most useful type of classification for the economic biologist.

Mr. B. L. Burtt said he was impressed by the similarity between the different views. Whereas Dr. Sprague defined taxonomy as a phylogenetic system, but in effect only claimed that taxonomic groups were monophyletic, it was highly probable that members of a group in a natural system, as defined by Mr. Gilmour, would be of common origin. Most concepts of a phylogenetic system involved hypothetical linkages between different groups, and there seemed to be general agreement among the speakers that such a classification was impossible in the absence of fossil evidence.

Dr. J. Burtt Davy, said that in his view attempts to produce a phylogenetic classification do not represent time wasted. A serious effort to acquire and piece together morphological, anatomical and cytological evidences of affinity leads to a more accurate evaluation of characters and affords excellent training, inspiring in the student a keen interest in taxonomy and putting life into what was—a half-century ago—a very dry and uninteresting subject.

Mr. M. J. D. White said that a more extensive cytogenetical study of selected groups of animals might be expected to provide new kinds of evidence for natural phylogenetic classifications. An investigation of the principles governing

the evolution of the sex-chromosome mechanism may prove to be particularly interesting in this respect.

In the genus *Drosophila* we can distinguish between a group of species with a rod-shaped (telocentric) X-chromosome and another group with a V-shaped (mediocentric) X. In the latter group (which is probably polyphyletic) a chromosome arm, which was originally autosomal, has become included in the X. It is highly unlikely that evolutionary steps of this kind are ever reversible. It remains to be seen whether the autosomal arm included in the X is the same one in all the species with mediocentric Xs.

A rather similar case in Praying Mantids is interesting because of its bearing on the phylogeny of the group. It has been shown that six genera (*Tenodera*, *Paratenodera*, *Hierodula*, *Sphodromantis*, *Mantis* and *Stagmomantis*) possess a complex sex-chromosome mechanism (X_1X_2Y in the males, $X_1X_1X_2X_2$ in the females). This mechanism has apparently arisen through the inclusion of a pair of autosomes in the sex-chromosome mechanism. This event probably resulted from a mutual translocation. Detailed study suggests that this must have happened only once, i.e. that the 191 species included in the X_1X_2Y group are all descended from a single ancestral XO species in which the translocation occurred. It is not often that one can be so certain that a large assemblage of genera and species is descended entirely from a single ancestral form, but whenever such cases are investigated they strengthen our confidence in the ultimate possibility of building up a natural phylogenetic classification, even where the geological record is discontinuous and fragmentary.

The PRESIDENT closed an interesting debate with a comment on the great diversity of view revealed and a remark that phylogenetic trees may serve in teaching if the student be cautioned that they are probably inaccurate.

PROCEEDINGS OF THE GENERAL MEETING
25 April 1940

Mr. J. RAMSBOTTOM, O.B.E., M.A., Dr.Sc., President, in the Chair

The Proceedings of the General Meeting held on Thursday, 11 April 1940, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted :—Arthur John Carpenter.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of Donald Albert Coult, Francis Charles Fraser and Kailas Nath Kaul.

Certificates of recommendation of the following candidates for Foreign Membership were read for the second time :—Prof. August Adriaan Pulle, of the University of Utrecht, and Dr. Thomas Barbour, of the Museum of Comparative Zoology, Harvard College.

Lt.-Col. R. B. Seymour Sewell, F.R.S., opened a Discussion regarding The extent to which the Distribution of Marine Organisms can be explained by and is dependent on the Hydrographic Conditions present in the great Oceans. [Printed in full below.]

Dr. Maurice Burton, Dr. Anna Hastings, Mr. J. R. Norman, Dr. Stanley Kemp, F.R.S., Dr. G. P. Bidder, Prof. W. Garstang and the President contributed to the Discussion ; Lt.-Col. Seymour Sewell replied.

The President expressed the thanks of the Society to the speakers.

The following paper was read in title :—

'Percy Sladen Expedition to Lake Titicaca, 1937. Scientific Reports.—VII. The Peruvian and Bolivian species of *Macrelmis* Motsch. (Coleoptera, Elmidae).' By H. E. Hinton, Ph.D.

THE EXTENT TO WHICH THE DISTRIBUTION OF MARINE ORGANISMS CAN BE EXPLAINED BY AND IS DEPENDENT ON THE HYDROGRAPHIC CONDITIONS PRESENT IN THE GREAT OCEANS, WITH SPECIAL REFERENCE TO THE PLANKTON.

By Lt.-Col. R. B. Seymour Sewell,
C.I.E., Sc.D., F.R.S., F.L.S.

When considering the possible extent to which the distribution of marine organisms is dependent on and can be explained by the hydrographic conditions present in the great oceans, it is essential to bear in mind the differences that exist between various great classes of the marine population.

Marine organisms are roughly subdivided into three main categories :—

(I) *Plankton*, organisms that possess little or no power of locomotion, and so drift passively with the ocean currents ;

(II) *Nekton*, organisms that are able to swim freely ; and

(III) *Benthos*, organisms that are attached to or crawl about over the sea-bed.

The *Plankton* is again subdivided into *Zoo-plankton* and *Phyto-plankton*, comprising the floating animals and plants respectively, and a similar division can be made in the *Benthos*. It must be borne in mind, however, that such a classification, though convenient, is to some extent artificial, for numerous species, both animal and plant, may belong to different categories at different stages of their life-history ; thus large groups of fixed animals, such as corals and sponges, that in their adult stage belong to the benthos, possess larval stages that are planktonic.

The plankton may be still further subdivided into *Neritic Plankton*, that inhabits the shallow water of the continental shelf, and *Oceanic Plankton*, that is found in the deep waters of the open ocean, and this last group is again subdivided into the *Epi-pelagic Plankton*, that frequents the upper levels, the *Meso-pelagic Plankton*, living in the middle depths, and the *Bathy-pelagic Plankton*, frequenting the deep water near the bottom. But here again the classification is artificial, since in many instances young stages are to be found at a level nearer the surface than the corresponding adults, so that a Meso-pelagic adult may possess Epi-pelagic Planktonic larvae.

The distribution of every marine organism must depend on the interaction of a number of factors, among which we may recognize :

(i) *Means of dispersal from one region to another.*—In those species of animals which do not possess planktonic eggs or larvae almost the only means of dispersal is by active migration, either of the animal itself or, in the case of parasitic forms, of its host ; in the great majority of marine organisms, however, the individual is planktonic at some period of its life-history, and to these the movements of the water masses in which it lives must be of considerable importance, the degree depending on the length of planktonic life.

(ii) *Suitability of environment.*—For those forms that are planktonic we include under this head such factors as the temperature, salinity, and oxygen-content of the water, the pressure to which the organism is subjected with increase of

depth, and perhaps to some extent the pH-concentration of the water. For those organisms that spend at least some part of their life on the bottom, whether free or sessile, we must also include the character of the sea-floor.

(iii) *Freedom from excessive competition.*—Under this heading we include direct competition between organisms that are mutually antagonistic, as in instances where one organism feeds on another or where both organisms require the same food-supply. We may also include here the presence of some organism that, in some way not yet understood, has an excluding effect, as has been suggested by Hardy and Gunther (1935) in their theory of Animal Exclusion for the interaction of phyto-plankton and zoo-plankton.

Finally we should include (iv) the *time factor*, namely the length of time that has passed since the first appearance of the species, for clearly an old-established species will have had more opportunity of reaching new areas of distribution than one that has only recently been evolved, though the distribution may at a later period again become curtailed and reduced by competition with younger and possibly better adapted species, or by geological or meteorological changes that destroy a part of the original habitat, as has been suggested in the 'Relict Theory', the organism surviving in isolated patches.

In past Geological Ages oceanic conditions were very different from what they are at the present day. At the present time there are two theories, held by different schools of thought, regarding the mode of formation and degree of permanence of the ocean basins. According to the older view the ocean basins are regarded as having always occupied, more or less, the same positions that they do to-day, though their interconnections were different, owing to the supposed presence of large land masses that have since undergone subsidence; the other view, the Continental Drift Theory of Wegener, holds that prior to the later part of the Cretaceous Epoch there was only a single continental mass, surrounded by oceans, of which the Pacific would to-day represent the remaining portion, while the Indian and Atlantic Oceans only came into existence at the commencement of the Tertiary Epoch as the result of fragmentation and drifting apart of the continental fragments (*vide* Holland, 1937). It would be out of place to discuss the relative merits of these two theories, though they must be borne in mind when considering the possible lines of dispersal of both animals and plants. Evidence is gradually accumulating that certain deep-sea areas are of comparatively recent formation; Umbgrove (1938) states that the present deep-sea relief of the East Indian Archipelago originated during

recent geological times, later than the Miocene, and I (1925) suggested that the Andaman Sea was formed about the Pliocene epoch : Wiseman and I (1937), in a joint paper, suggested that the Arabian Sea assumed its present form in Tertiary times, and that its northern part originated by subsidence in Pliocene or post-Pliocene times ; all these areas therefore must have been populated originally by species that were in existence at that time, and their formation may have provided the necessary stimulus for the evolution of new species. The region of the Malay Archipelago has long been known as an area of species-formation, and it is of particular interest, if we accept the view that the Atlantic Ocean is of comparatively recent formation, commencing in the late Cretaceous and being completed in the commencing Oligocene (*vide* Gregory, 1929), to consider the extent to which this too may have been a stimulus for the production of new species.

Whichever view is the correct one, it seems certain that during the early part of the Tertiary Epoch there was in existence a large sea, the Tethys, that extended from the Indo-Pacific region on the east across the Gangetic plain of India and the present line of the Himalaya mountains and then along the Mediterranean basin to what is now the North Atlantic, while from this great east-and-west sea a northern arm established a direct connection with the Arctic Ocean ; at the same time there was a direct connection between the tropical Atlantic and Pacific Oceans across what is now Central America. We have no actual information regarding the trend of the oceanic circulation at this period, but it seems clear that there must have been a flow of warm water from the Indo-Pacific region through the Tethys Sea into the Atlantic Ocean and on into the east Pacific. Wayland Vaughan (1919) has pointed out that as long as this cross connection was in existence, from the Eocene to the middle or even late Miocene, the coral faunas of the Indo-Pacific, the Atlantic and the east Pacific regions were identical, but with the closure of the Tethys and the upheaval of Central America the corals of distinctive Indo-Pacific facies became extinct on the Atlantic side. He gives a list of twenty-eight Indo-Pacific genera that are now absent from the west Atlantic, and of these fifteen were present in both regions in Oligocene times. Crossland (1928) has also commented on the paucity of the coral fauna of the eastern Pacific, and has given a list of sixteen genera that are absent from Tahiti in the east Pacific, but are present in Samoa and Fiji in the west Pacific, and of these eleven are contained in Wayland Vaughan's list.

Indo-Pacific genera of corals not living in the Atlantic. Those marked * were formerly present in Oligocene times (Wayland Vaughan, 1919).	Indo-Pacific genera of corals not living in Tahiti (Crossland, 1928).
**Pocillopora.*	
**Stylopora.*	
**Euphyllia*	*Euphyllia.*
**Galaxea*	*Galaxea.*
**Antillea.*	
**Favites*	*Favites.*
**Hydnophora*	*Hydnophora.*
**Leptoria*	*Leptoria.*
**Symphyllia*	*Symphyllia.*
**Pavona.*	
**Leptoseris.*	
**Haloseris.*	
**Diploastrea*	*Diploastrea.*
**Astreopora*	*Astreopora.*
**Goniopora*	*Goniopora.*
Seriatopora	*Seriatopora.*
Cyphastrea.	
Leptastrea.	
Fungia.	
Herpetolitha.	
Polyphyllia.	
Halomitra.	
Podobacia.	
Pachyseris.	
Coeloseris.	
Psammocora.	
Turbinaria	*Turbinaria.*
Montipora.	
	Acrohelia.
	Echinopora.
	Goniastrea.
	Coeloria or *Meandra.*
	Merulina.

Crossland thinks that this distinction between the eastern and western Pacific corals ' is what would be expected from the fact that the main surface currents are from east to west, directly against the spread of coral larvae from the centres of distribution in the Malayan and Australian regions ', and the disappearance of the Indo-Pacific corals from the West Indies can be accounted for by the interruption of the westwardly-flowing water through the Tethys Sea owing to the upheaval of the Himalayas and from the Atlantic into the Pacific by the uprising of central America ; so long as these currents persisted coral larvae could be carried in successive generations from one area to the other, but with their interruption this supply would automatically cease.

Børgesen (1934), when studying the Algae of the coast of western India, was struck by the number of species, 68, or 59·6 per cent., that are common to this region and the North Atlantic and Mediterranean, and he attributes this to the

former existence of the Tethys Sea ; he, however, thinks that the dispersal was from the Atlantic to the Indian region. Previous observers had also been struck by these similarities, and Murray (1893) put forward the suggestion that it was due to a periodic mingling of the flora of the two regions round the Cape of Good Hope ' during epochs in which the climate of the Cape was considerably warmer than it is at the present day '. Svedelius (1906), while admitting that several forms common to the Indo-Pacific region and the Mediterranean must have entered the latter from the south-east, attributed the similarity of the Indo-Pacific and North Atlantic regions to the former presence of the connection in early Tertiary times between the Atlantic and Pacific Oceans across Central America.

It seems unlikely that the closure of the Tethys Sea in the middle of the Tertiary Epoch could have produced such a dissimilarity in the coral fauna of these two regions and yet have permitted the persistence of such a degree of similarity in the algal flora. Børgesen moreover entirely ignores the fact that of the algal species recorded by him as common to the Atlantic and Indian regions, no less than 35 per cent. are known to occur at the Cape of Good Hope, and it appears highly probable that these have, as suggested by Murray, been carried round in the surface currents.

The direct connection in early Tertiary times between the Tethys Sea and the Arctic, and, at a later period, the cooling of the water of the North Atlantic Ocean during the Glacial Epoch, must have permitted the dispersal of species from one area to the other, in the first warm-water species being able to penetrate far to the north and in the second cold-water species spreading far to the south of their present-day distribution ; the occurrence of several so-called Arctic Copepoda in the Mediterranean Sea and its offshoot the Adriatic Sea has been regarded by some as an example of an Ice-Age Relict Fauna, but Pesta (1920) has given a word of warning against this hypothesis and regards it as entirely unproved.

Several zoologists, who have studied the fauna of moderate depths in the Indian Ocean, and especially in the Arabian Sea, have been struck by the occurrence of species that were previously known only from the Atlantic or the Mediterranean Sea. Alcock (1898) gave a list of forty-one such species, belonging to the Coelenterata, Mollusca, Crustacea and Pisces, in depths ranging from 130 to 1997 fathoms (240 to 3650 metres), and he attributed this apparently discontinuous distribution to the former existence of the Tethys Sea, assuming that in Tertiary times these species were distributed throughout the whole area, but that with the upheaval of the Alpine-Himalayan mountain range and the

consequent obliteration of the central region they became isolated at the two extremes and, owing to the persistence of similar conditions in the deep water of both areas, have not undergone any evolution *.

More recent work has greatly increased the number of species that are now thought to have a similar distribution, and are apparently confined to the North Atlantic Ocean and the Arabian Sea, though some are also found in the Mediterranean Sea. Among the Indian Polychaeta, which have been reported on by Fauvel (1932) and Monro (1937), many of the species are cosmopolitan, but between the depths of 73 to 1435 metres there occur fourteen species whose distribution is confined, so far as we know, to these regions, with two exceptions that extend as far east as the western Pacific Ocean. Of these fourteen species no less than twelve have been taken in the Mediterranean, and this may well be claimed as evidence that the distribution is to be accounted for by the former existence of the Tethys Sea, though it could equally be accounted for by a migration from the Indian Ocean through the Red Sea and the present or a former connection between this and the Mediterranean Sea into this latter area and on into the North Atlantic.

Among the Crustacea Stubbings (1936) has recorded four species of the genus *Scalpellum* from depths between 222 and 3775 metres that occur in the North Atlantic and the northern part of the Indian Ocean, and of these three show an extension to the western Pacific Ocean. Barnard (1937), in his report on the John Murray Amphipoda, has recorded five species that occur in the North Atlantic, even as far north as Iceland, and in the Arabian Sea, and he tentatively ascribes their distribution to the former existence of the Tethys Sea. He (1936) has also recorded from the Arabian Sea and the Maldive Archipelago an Isopod previously known only from the North Atlantic and the Arctic, but in this case he remarks ' it would probably be straining speculation too far to regard this latter species as a relic from the days of the Cretaceo-Tertiary sea of Tethys '.

In the Mycidacea Tattersall (1939) has recorded the occurrence of a species, *Petalophthalmus oculatus* Illig., from the Carribean Sea and the Arabian Sea, and, like previous authors, has attributed this to the Tethys Sea.

In the decapod *Natantia* Kemp (1910) recorded four species that were known from the North Atlantic and the northern part of the Indian Ocean, and of these three occur farther east in the western or central part of the Pacific Ocean.

In the Penacidae Ramadan (1938 *a*) has recorded five species

* Since the publication of Alcock's list several of the species have been reported from the region of the Cape of Good Hope,

with a similar discontinuous distribution, and the same author (1938 *b*) has added another species among the Palinura.

Among the mid-water Calanoid Copepoda I have found no less than thirty-one species that are at present known only from the North Atlantic and the Arabian Sea; and, if we include the South Atlantic and the Bay of Bengal in the distribution, there are fourteen others, making a total of forty-five, known only from the Atlantic and the northern part of the Indian Ocean.

Norman (1939) has added several species of fish, namely:

Xenodermichthys copei Gill, from 457–658 m., from the Atlantic Ocean and Zanzibar;

Avocettinops schmidti Roule and Bertin, 1207–1463 m., from the Carribean Sea and Zanzibar;

Nansenia groenlandica (Reinhardt), 494–658 m., from the N. Atlantic Ocean, Zanzibar and the Maldives;

Venefica proboscidea (Vaillant), 1899 m., from off Morocco, the Arabian Sea and the Gulf of Manaar;

the last two having also been taken off South Africa.

As long as only a comparatively few species were known to have this apparently discontinuous distribution, the theory that it could be accounted for by the former existence of the Tethys Sea was a plausible one, but we are now faced with the paradox that, as more and more species are found to inhabit these regions, the less probable does the explanation become.

It must be borne in mind that such evidence as we now have indicates that the fauna of the deep sea is of comparatively recent origin. Farran and Calman (1928) sum up our present knowledge in the following words:—'On account of the general resemblance of the abyssal fauna to the animals inhabiting shallow water at the present time, rather than to those of a remote geological period, it is generally believed that the inhabitants of the deep sea have migrated thither at some comparatively recent geological age, the migration probably beginning at the close of the Mesozoic Period and continuing to the present day.' I have already mentioned that there is evidence to suggest that the North Atlantic Ocean itself is a comparatively recent formation, and only came into existence in the late Cretaceous and early Tertiary Epochs, its formation coinciding with the obliteration of the Tethys Sea. This obliteration can thus provide an adequate explanation for the discontinuous distribution of only such species as were already in existence in the first half of the Tertiary epoch, and can have had no effect on the distribution of species that arose at a later period. We must therefore look for some alternative explanation, and one ancient group that might be expected to give us a clue to this is the Crinoids. Our knowledge of the

distribution of this group is largely due to the work of Austin Clark (1912, 1913, 1936), and it seems that we can trace two definite lines of dispersal, though the actual causative agent was probably the same in each. In former times, when there was a direct connection between the Indo-Pacific and the North Atlantic regions through the Tethys Sea, and a further connection from the Indian Ocean to the Arctic, a number of species made their way from the Malayan Region in both directions; but another group has passed from the Malay region across the Indian Ocean and then up the African coast to the Gulf of Oman, while the Crinoids of the East African region extended westward into the Atlantic Ocean, then up the west coast of Africa and across to the West Indies, *via* St. Helena, and finally down the east coast of South America from Venezuela to southern Brazil. These latter lines of dispersal appear to me to coincide very closely with the general trend of the surface currents, and Clark himself (1913) suggests that the extension southwards of the Crinoid species of the western Atlantic and the corresponding extension northwards of the species of the eastern Atlantic is the result of the action of the deep-water currents along the two coasts.

Thanks to the work of numerous expeditions and the co-operation of many observers in the navies and merchant services of all civilized countries it has been clearly shown that in each of the great oceans there is present a series of water masses, lying at different depths and moving in different directions, and each characterized by differences in salinity, temperature, oxygen-content and pH-concentration. On the surface in the tropical and temperate regions there is a layer of warm surface-water; immediately below this lies a mass of water, the Sub-Polar Intermediate Current, that is passing northwards in each of the great oceans and that has its origin in the region of the great West Wind Drift; below this again in the North Atlantic we have a large mass of water, the North Atlantic Intermediate water, that is flowing southward; in the Pacific Ocean the corresponding mass of water is relatively very small, and in the Indian Ocean it is replaced by the Indian tropical Intermediate water; finally, on the bottom we get the Antarctic Bottom Drift that originates in the Antarctic region and flows eastwards and northwards.

In the tropical and temperate regions the surface water, under the influence of the prevailing winds and the rotation of the earth, moves in a series of circular currents that run clock-wise in the Northern Hemisphere and counter clock-wise in the Southern (*vide* Schott, 1926; Wüst, 1928; and Schott, 1935), and between these two systems lies a contra-equatorial current running from west to east. From the northern system in the Atlantic Ocean a branch passes towards the

north-east, the North Atlantic Drift, and this can be traced up past the British Isles and the coast of Norway into the Arctic, while a cold current, the Labrador Current, sets out of Baffin Bay down the East coast of North America. In the Pacific we get a very similar set of currents; here again we have north and south circular movements, but in this ocean no branch from the north circular system can pass into the Arctic, though a cold current sets southwards through the Bering Sea and along the Asiatic coast, the Okhotsk current. In the Indian Ocean conditions in the northern region are reversed every six months owing to the alternation of the North-east and South-west Monsoons, but south of the Equator we have a circular movement similar to that in both the Atlantic and Pacific Oceans, and, especially during the North-east Monsoon, some of this water passes in a branch of the Agulhas Current westwards past the Cape of Good Hope into the South Atlantic Ocean. In addition to this southerly connection there is also a connection between the Indian and Atlantic oceans up the Red Sea and through the Suez Canal and the Mediterranean Sea (*vide* Fox, 1929, Appendix 1), the current flowing northwards in the Suez Canal during at least nine months of the year; very little surface water, however, can pass from the Mediterranean Sea into the Atlantic, for, as Schott (1928) has shown, the prevailing current through the Straits of Gibraltar is from the Atlantic eastward into the Mediterranean Sea. Between the Pacific and the Indian Oceans there are numerous channels between the islands of the Malay Archipelago whereby surface water can pass from one ocean to another, the direction of flow being reversed with the change of the Monsoon winds.

Further south between lat. 40° and 50° S. we get a continuous flow of water, the West Wind Drift, from west to east round the whole circumference of the globe; and finally in the extreme south lies the polar current that tends to move in two circular clock-wise systems, the water passing westwards along the Antarctic coast and turning right-handed to flow eastward, parallel to the southern boundary of the West Wind Drift.

It is now generally recognized that the character and direction of flow of the marine currents have had a profound influence on the fauna and flora of different regions, and this has enabled zoo-geographers to divide the surface of the globe into a number of areas, as shown in the map given in 'The Science of the Sea', published by the *Challenger* Society, 2nd edition, 1928. The effects of these currents are particularly noticeable in four regions; the north-easterly flow of the North Atlantic Drift causes an extension far to the north of the region of the North Atlantic Ocean, while the Brazilian current

causes a similar extension to the south-west of the South Atlantic Ocean area: the southward flow of warm water along the north-west coast of Australia extends the region of coral-growth far to the south, and this region is split off from the Indian Ocean area and is classed with the Malay Region; and finally, the penetration far to the north of the Peruvian Current and the consequent extension northwards of species characteristic of the Antarctic has given rise to the separation of an Eastern Pacific Region.

That the surface currents have a profound influence on the distribution of the Plankton has long been recognized, and Pelseneer (1887) remarks 'it seems to me that each great surface area of water coinciding with an important current or system of currents, forms a distinct pelagic province'. (For a summary of previous investigations on this subject *vide* Giesbrecht, 1892.)

Where these great current systems abut on each other we get what are termed 'Convergence Zones', and a certain amount of mixing of the water masses takes place; but where one current is a warm one and the other cold the change of temperature acts as a barrier across which it is difficult for organisms to pass. A somewhat similar area of admixture lies to the south-west of the Cape of Good Hope, where a branch of the warm Agulhas Current meets both a branch of the cool water of the West Wind Drift and also cold upwelling water, the combination of these different waters forming the Benguela Current. Meisenheimer (1905) called attention to this region, which he termed the 'Sud-Afrikanischer Mischgebiet', and the work of Stephenson and his colleagues (*vide* Stephenson and du Toit, 1937, and Isaac, 1937) has shown clearly that there is here a marked change in the littoral fauna and flora, clearly correlated with the distribution of the water masses, eastern forms being prevented from spreading westward: and it has been maintained that here the warm-water plankton coming from the east is killed off. Such a region must, at least to some extent, prove a barrier to the passage westward of plankton from the Indian Ocean, but it seems to me that its efficacy has been somewhat exaggerated and that a number of the more hardy species are able to survive.

On the other hand, the work of the Cambridge Expedition to the Suez Canal, 1924 (*vide* Fox, 1929), has clearly shown that numerous species are spreading north-westward from the Indian Ocean through the Red Sea and the Suez Canal into the Mediterranean Sea.

Within the limits of a single ocean detailed studies of the fauna and flora or of single organisms have in recent times shown that in many instances the distribution can be correlated with the presence of water of a particular origin

and the direction of flow of this water. Such a correlation was investigated by Cleve (1900) for both Phyto- and Zoo-plankton in the North Atlantic. Damas and Koefoed (1907) are of the opinion that it is only under certain conditions, such as a sudden and periodical appearance of unusual forms, or the dispersal of species that are known to inhabit and reproduce in a limited area, either of locality or of depth, that species can be used as indicators of currents; and that most deep-sea species are too widely distributed to serve as indicators.

More recently Russell (1935 *a*, 1935 *b*) has indicated the extent to which certain planktonic organisms can be used as indicators of the movement of different bodies of water, and in the later paper he has referred to the work of several previous authors who have correlated the distribution of planktonic organisms with the movements of surface or deep currents. Kemp (1938), in his Presidential Address to Section D of the British Association at Cambridge, drew attention to a series of papers in which authors have shown a direct connection between the abnormal influx of Atlantic water into and through the English Channel and the presence of unusual planktonic organisms of Atlantic origin in the North Sea: and I need hardly remind readers of Schmidt's work (1932) on the way in which the Leptocephali larvae of the European Eel are carried eastward across the Atlantic from the Sargasso Sea to the European coasts. It is even possible that such large animals as Turtles may be carried across the North Atlantic by the Gulf Stream and North Atlantic Drift (*vide* Parker, 1939). All the above work has been carried out in the North Atlantic region, but a similar correlation has been shown to exist in the Southern Ocean, as evidenced by the distribution of the Diatom *Rhizosolenia curvata* Zacharias (*vide* Hart, 1937).

Evidence is gradually accumulating that the distribution of benthonic organisms may also be affected by currents: Reid (1935) pointed out the correlation between the occurrence of the Sea-urchin, *Echinus esculentus*, in the littoral zone and the flow of the North Atlantic Drift, and Moore and Kitching (1939) have attributed the distribution of the Barnacle, *Chthamalus stellatus*, around the British Isles to the same cause. Similarly the studies of Fischer-Piette (1936) on the distribution of the fauna and flora of the English Channel have shown that many organisms extend up the Channel as far as the Isle of Wight, and there disappear, and it seems possible that this eastward limit is correlated with the flow of the tidal currents that enter the Channel at its two ends and neutralize each other in or near the Isle of Wight region. But perhaps the most striking example of the way in which the distribution

of a group of sessile organisms may be explained by water movements is to be found in three papers on marine sponges by Burton (1930, 1932, 1934); in the first of these he points out that 'the distribution of littoral species is, or may be, reasonably supposed to be influenced considerably by the fact that Sponges, like any other group of marine animals, are able to creep round the coasts. For species in deeper waters, however, the deciding factor appears to be the main surface-currents of the Ocean', and he shows that so far as the Atlantic and Arctic Oceans are concerned the trend of the surface currents provides a very complete explanation of the distribution of these animals. In the second paper (1932) he shows that the same explanation can be applied to the sponges of the South Atlantic and Indo-Pacific regions, but that the barrier off the Cape of Good Hope has allowed only two species to pass from the one ocean to the other; in his last paper Burton (1934) states that, as regards the distribution of the sponge-faunas of the Indian Ocean and the Malay region, 'so far as can be seen at present, the line of their distribution follows through from the Malay area and Indian Ocean round the most southerly point of the African continent, up its west coast to the Azores and thence into the West Indies on the one hand and the Mediterranean on the other'.

It is widely held that the Epi-pelagic plankton of tropical and subtropical regions has, as a rule, a world-wide distribution; Ekman (1935) states that owing to the current movements there is a moderate degree of homogeneity in the fauna of the warm water, and that for the greater part this distribution is circumterrestrial: Bedot (1909), however, went even further, and maintained that this dispersal is so free that any difference that is found to exist in different regions is purely temporary. The Copepod genus *Copilia*, as has been pointed out by Lehnhofer (1926), has achieved a distribution that clearly corresponds to the surface currents in the Indo-Atlantic tropical region; but a study of various other animal groups indicates that a distribution of this type is usually only partial. The Salps, for instance, the distribution of which (*vide* Apstein, 1905, 1906; and Metcalf, 1918) depends on the hydrographic relations of the currents, the temperature and the salinity, are by no means all cosmopolitan; two species are known only from the Pacific Ocean and one from the Indo-Pacific region, one is known only from the Indian and Atlantic Oceans, one is confined to the Atlantic and another to the West Wind Drift, while the remaining seventeen occur in all three great oceans, and of these nine have succeeded in getting into the Mediterranean and one to the Antarctic. Thus out of twenty-three species eighteen have succeeded

in getting round the Cape of Good Hope and three have got as far north in the Atlantic as Greenland, Iceland and the Hebrides.

Steuer (1933) has compiled a chart, based on the distribution of the surface Copepoda, dividing the oceans into regions and sub-regions, and a comparison of this with the chart of the ocean currents at once reveals so close a degree of similarity that it is impossible to avoid the conclusion that the one depends on the other. Commencing from the north, Steuer's arctic region covers the cold water of the Arctic Ocean and its southern continuations in the Labrador and Okhotsk currents; the subarctic Atlantic region is the region of the Gulf-stream and the North Atlantic Drift, while the sub-arctic Pacific region corresponds to the Kuro-Siwo and Californian currents; the northern tropical Pacific and Atlantic sub-regions correspond to the North Equatorial currents in these oceans; the southern sub-tropical sub-regions correspond in each of the oceans to the southern part of the circular movement of the water; the circumpolar antarctic region corresponds to the West Wind Drift; and finally, the antarctic region corresponds to the true South-polar water.

In attempting to trace any correlation between the movement of the water masses and the distribution of marine organisms it is essential that we should have, first, a fairly definite knowledge as to the region in which the species or genus first made its appearance, and, secondly, the depth at which the species normally lives, since, if the dispersal be due to currents, the direction in which the organism will be transported will differ at different depths. Steuer (1933) has pointed out that the Southern Hemisphere, with its wide stretches of ocean, is favourable for the development of oceanic species; he also points out that a number of Atlantic genera and subgenera are found also in the Indo-Pacific region, and that in such cases the Indo-Pacific forms are the more primitive. The region of the Malay Archipelago has long been regarded as a locality in which there has been a profuse evolution of new species and genera, and, if the number of species and genera present in this area to-day is any criterion, then it seems clear that a very large percentage of both littoral weed-haunting and surface-living Copepoda have had their origin in this region and must have spread thence into other areas. If this dispersal be due to the movement of the water masses we should expect to find that the further we get away from the original home the fewer of these species will be found.

In a recent paper (1940) I called attention to the manner in which the percentage of Indo-Pacific species among the weed-haunting littoral Harpacticidae gradually decreases as

we pass westwards round the Cape of Good Hope into the Atlantic Ocean and along its main current systems, or up the Red Sea into the Mediterranean Sea, and, moreover, that this change in the fauna agrees well with the distribution of Indo-Malayan Algae, so that it is probable that both have been carried along together. The same gradual falling off in the number of Indian species is to be found in the surface-living Calanoida. I have taken the depth of 400 metres as the dividing line between these Epi-planktonic forms and the Meso-planktonic species for several reasons: first, it is at this depth that plant-life ceases from lack of light, and it is also approximately the depth at which the warm upper water is on the average separated from the colder deeper water. This depth also corresponds to the level that separates the two upper divisions of Haecker (1908), the Phaoplankton and Knephoplankton, from the two deeper layers, the Skoto-plankton and Nyktoplankton.

A preliminary survey of the surface-living Calanoida shows that in the east Pacific region out of a total of fifty-eight species there are eight that appear to be endemic, one has only got as far as the south-west Pacific, five have reached the Indian Ocean, and thirty-nine have reached the Atlantic: in the south-west Pacific region sixteen species appear to be endemic, fifty-nine have reached the Indian Ocean, but twenty-eight have got no further. In the Indian region I have records of no less than 167 species; of these seventy-seven, or less than half, are known from the Atlantic Ocean, thirty-seven have colonized the South Atlantic, seventeen have reached the West Wind Drift, and three have penetrated into Antarctic waters; sixty-three species have been taken in the Tropical Atlantic, but of these ten appear to have got no further; as many as sixty species have now been taken in the North Atlantic Ocean, and of these thirty-six have been taken in the Mediterranean Sea, twenty-eight have reached the Woods Hole region of the American coast, twenty-two have got to the British Isles, seven are known from the coasts of Norway and six have got as far as the Arctic. Following the alternative route westward, fifty-seven species have got into the Red Sea, and of these nineteen have passed into the Suez Canal and may have reached the Mediterranean Sea by this route instead of from the North Atlantic. A comparison of these figures with those of the weed-haunting Harpacticids indicates that here too the distribution has been by means of the surface currents. There are, however, a few species that have not been taken in intermediate areas, three from the East Pacific and North Atlantic, five from the Indo-Pacific region and the tropical or North Atlantic, and three from the Indian Ocean and the North Atlantic; and it is thus possible that these eleven

species may represent a relict fauna from the Tethys Sea or the former connection between the Atlantic and the Pacific Oceans across Central America, but it is probable that further investigations will reveal their presence in intermediate localities.

Turning now to the deeper levels, we have already seen that in each ocean at least three masses of water, lying at different levels and having different origins, can be detected (*vide* Defant, 1930). The first of these is the South-polar Intermediate water; in the southern hemisphere this mass of water sinks down from the surface between roughly 40° and 60° S. under the West Wind Drift and then turns northwards towards the Equator, flowing up into each great ocean at a depth of about 500–1500 metres. In both the Atlantic and Indian Oceans this South-polar Intermediate water can be traced beyond the Equator into the northern hemisphere (*vide* Wüst, 1928, and Defant, 1930, for the Atlantic Ocean, and Mohamed, 1940, for the Indian Ocean); in the Pacific this deep current does not extend so far to the north, and fails to reach the Equator, but the work of the 'Snellius' Expedition has shown that certain basins in the Malayan Archipelago, namely Boeroe Basin, Banda Basin, Wetar Basin and Sawoe Basin, are filled with water that is flowing in from the Pacific Ocean at a depth of less than 1500 m. (*vide* van Riel, 1934, 1938), and this must be derived from the South-polar Intermediate current. In the Atlantic Ocean the main mass of this water lies on the west side close against the South American continent, and probably the same is true of the Indian and Pacific Oceans, since this westward trend is dependent on the effect of the spin of the earth. In the North Atlantic Ocean the spin of the earth imparts a right-handed trend to the movement, and in consequence some of this water swings across the Atlantic Ocean and, as has been shown by Pettersson (1927), tends in the neighbourhood of the Cape Verde Islands to rise towards the surface. In the Indian Ocean in the northern hemisphere some of this water swings westward into the Gulf of Aden, but the bulk of it turns eastward across the Arabian Sea.

The next mass of water to be considered arises in the Northern Hemisphere. In the Atlantic this mass originates by a sinking down of surface water between 20° and 60° N., augmented by a deep current of Arctic water that is flowing southward from Baffin Bay through Davis Strait (*vide* Wüst, 1928); this mass of water flows in the main along the American coast lying at a depth of 1500–4000 m., the main stream being between 2000 and 3000 m., and in about 20° N. it is joined by water that originated in the Mediterranean Sea and has drifted in a south-westerly direction across the North Atlantic.

In the Southern Hemisphere this current develops an eastward trend and tends to spread out ; one branch passes to the Gulf of Guinea and another flows right across the whole width of the South Atlantic Ocean in about 30° S. and is then continued past the Cape of Good Hope into the Indian Ocean, where it has been detected at a depth of about 3000 m. (*vide* Clowes and Deacon, 1935) ; finally, the remaining mass of water tends to rise towards the surface in the Antarctic and mixes with the Antarctic water. In the Indian Ocean a corresponding mass of water arises in the northern part of the Arabian Sea and in the Bay of Bengal, partly by sinking down (*vide* Sewell, 1932) and partly by an outflow from the Gulf of Oman, the Red Sea only contributing a very small percentage and more in winter than in summer (*vide* Thompson, 1939, and Mohamed, 1940).

In the Arabian Sea this mass of water extends from some 600 m. down to nearly 3000 m., but to the south of the Equator it lies in the main between 2000 and 3000 m. ; the southerly flow appears to be largely influenced by the Carlsberg Ridge, for in the western region this water only reaches, according to Thomsen (1933), as far as about 10° S., but Clowes and Deacon (1935) have traced it as far as 20° S. Deacon (1937) has summarized our knowledge up to the time of his report, and he shows that there are indications in the south-eastern part of the Indian Ocean of a mass of water, moving eastwards into the Pacific, that appears to be derived in part from the Indian Tropical Intermediate water moving towards the south-east and in part from the Atlantic water moving east across the whole width of the Indian Ocean ; and both Sverdrup (1931) and Schott (1935) are of opinion that the water of the southern Pacific Ocean at a depth of 1500 m. does not originate in that ocean but is an importation from the depth of the Indian Ocean and even further westward from the Atlantic Ocean. The mass of this Atlantic-Indian water lies in the south-western part of the Pacific Ocean at a depth of about 2000 m., and it seems probable that some at least of this water, possibly mixed with Antarctic bottom water, passes northwards and, curving round to the west under the influence of the earth's spin, enters certain of the deeper basins of the Malay Archipelago, which van Riel (1938) has shown to be filled with water from the Pacific at a depth of about 2500 m.

In the Pacific Ocean there is no mass of Intermediate water, corresponding to the Atlantic and Indian Intermediate currents, but a comparatively small mass of Arctic water appears to make its way southwards in the Okhotsk Current, and is found between 15° and 50° N. at a depth of 500–1500 m. ; it seems probable, however, that there is a southward

movement of water below the South Polar Intermediate water, similar to that found in the other two oceans, and that some at least of this water passes eastward between Cape Horn and the Antarctic continent, though it is doubtful if it actually enters the Atlantic Ocean, for, though Clowes (1933) believes that it flows across the South Atlantic, Deacon (1937) thinks that it does not get beyond the Scotia Arc.

Finally, flowing along the bottom is the Antarctic Bottom Drift, formed by a mass of water that in the main has its origin in the Weddel Sea ; from there the current passes eastward and northward, flowing up into each of the great oceans : owing to the depth at which it lies its direction is markedly influenced by the configuration of the bottom ; thus, on the west side of the Atlantic it can pass freely northward as far as or even beyond the Equator, but on the east side its passage northward is barred by the Walfisch Ridge. In the Indian Ocean it appears to pass northward in three main streams (*vide* Sewell, 1932, Wüst, 1934, and Mohamed, 1940) ; the most westerly passes between Madagascar and the Seychelles, the middle stream flows between the Seychelles and the Carlsberg Ridge, and the third flows northward on the east side of this ridge and the Mid-Indian Ridge into the Bay of Bengal, a branch swinging westward to enter the Arabian Basin between the Maldive and Chagos Archipelagoes. The last part of the Antarctic Bottom Drift enters the Pacific Ocean, passing eastward to the south of Australia and New Zealand.

As with the surface currents, where two streams of water of different origin impinge on one another there must be a certain, and possibly a considerable, amount of intermixing ; but in these deeper levels such an admixture can produce only very slight changes in temperature, salinity, pH-concentration or oxygen-content, and in consequence would have little or no restraining influence on the free passage of organisms from one stream to another. Indeed, with any interchange of water a corresponding interchange of the plankton must take place ; furthermore, as I have already mentioned, the larval stages of many species are known to occur at a higher level than that usual for the adults. Schmaus and Lehnhofer (1927) have shown this very clearly in the case of the three species of the genus *Rhincalanus* (Copepoda), and Stiasny (1934) is of the opinion that young stages of the Scyphomedusa, *Periphylla hyacinthina*, are found much nearer the surface than the adults : he remarks ' it is in general no doubt true that in *Periphylla* the size increases with the depth ; because during development the medusa sinks from shallow into deeper layers.' Fraser (1936) has suggested that the distribution of *Euphausia superba* is due to ' the rotary movement resulting

from the assemblage of the earlier developmental stages in the southward flowing warm deep water and that of the later stages in the northward flowing Antarctic surface water'. Thus a planktonic organism might be carried from the North Atlantic Ocean to the South Atlantic, as has been pointed out by Russell (1935 *b*), and thence round the Cape of Good Hope and on into the southern regions of the Indian and Pacific Oceans without experiencing any appreciable change in either salinity or temperature, and by a slight change of level either upwards or downwards, in most cases probably the former, can pass into another current that will transport it northwards again into the tropical regions of either the Indian or Pacific Oceans. It is important to recognize, however, that, so far as our knowledge goes at present, there is no current of water, whether surface or deep, that could carry plankton from the Atlantic Ocean directly into the Pacific round Cape Horn, for here the whole mass of water from the surface to the bottom is moving eastward.

If such an interchange of fauna is taking place, we should be able to find some evidence of it, similar in character to the evidence that we have already noted in regard to the surface plankton. A study of the deep-water Calanoids shows clearly that if the number of species present is any guide, then the centre of evolution of this group lies not in the Indo-Pacific region but in the North Atlantic Ocean, where some 350 species are now known to occur, as compared with 185 in the Indian Ocean and 232 in the Pacific. Nordgaard has suggested that boundary areas, such as the North Atlantic, where warm and cold currents meet, are centres of species building, and that if this be so then such areas will be centres of species distribution; and Lysholm and Nordgaard (1921) have commented on the way in which the currents meet in the North Atlantic and the number of species of Copepoda that have been described from the North Atlantic Slope. The same evolution of new species appears to have occurred in this region in other groups, for Nordgaard was working on Bryozoa, and Robson (1924), in a Report on the Cephalopoda of the South African waters, remarks: 'I am inclined, on the whole, to support Clark in his contention that the Abyssal forms (of Crinoids) of the South African fauna are probably of North-western origin. With regard to the deep-water Polypoda and species of *Cirroteuthis* I certainly consider them to be most closely related to North Atlantic forms'.

Among the Meso-planktonic Calanoida of the North Temperate Atlantic Region are some eighteen species that have been carried in from the Arctic by the Labrador Current: and conversely ten species have been carried from the Atlantic into the Arctic Ocean over the Faroe-Iceland and Wyville Thompson

Ridges by the North Atlantic Drift; but, as Russell has pointed out, a large number have been carried southward in the North Atlantic Intermediate current: some forty-two species have reached the sub-polar region of the Antarctic, and of these thirty-four appear to have been carried northwards again into the Indian Ocean, and twenty-three species have reached both the Indian and South-west Pacific regions, six others have reached this latter area, and eighteen have got into the East Pacific region; the numbers thus decrease from west to east in a series 34, 29, 18. Numerous other species appear to have been carried eastward without appearing in the sub-polar area: of these forty-five have passed into the Indian Ocean, but have got no further, fifty-one others have reached both the Indian and South-west Pacific regions, and of these ten, or 20 per cent., have been taken off the Cape of Good Hope: finally, thirty-three of these have reached the East Pacific area. Some thirty other species have been recorded from the Atlantic and South-west Pacific but from no intermediate area; the direction in which these have travelled must therefore for the present remain uncertain, but in view of the fact that the deep water round Cape Horn is drifting eastward it is impossible for these species to have been carried in directly from the South Atlantic, and we may assume that they too have passed eastward across the southern part of the Indian Ocean. Here again the numbers of Atlantic species decrease as we pass eastward, namely, 157, 133 and 55. Twenty-nine species appear to have arisen in the Indian Ocean, and of these fourteen appear to be endemic, so far as our present knowledge goes, and fourteen species have spread to the South-west Pacific region and two to the East Pacific. Thirty-nine species appear to have had their origin in the South-west Pacific region, and of these four have reached the East Pacific region and five seem to have got into the Atlantic. Finally, thirty-seven species have been evolved in the East Pacific area, and of these four have reached the Atlantic Ocean.

It seems to me that one is justified in claiming that the evidence points strongly to a dispersal of these Meso-planktonic species along the deep currents, and especially southwards along the North Atlantic or the Indian tropical Intermediate currents and then northwards again in the South-polar Intermediate water; that very few species appear to have got from the Pacific to the Atlantic Ocean is in agreement with the view that deep eastward-flowing Pacific water does not get beyond the Scotia Arc.

A number of species of Copepoda are known to migrate vertically, in many instances diurnally, and if such species are living near the boundary between two different layers of

water such a migration may easily carry them from one current to another. Species that normally occur in the surface warm-water stratum may descend to such depths that they pass beyond the zone in which the stimulus to ascend again can act, and Russell (1930) has asked whether such individuals are lost. I have already suggested that mid-water species can be carried from the Atlantic Ocean into the Indian Ocean by the North Atlantic Intermediate water, and it seems probable that certain species that are normally confined to the Atlantic surface stratum may thus be carried into the Indian Ocean. Five such species, namely *Calanus finmarchicus*, *Pontella atlantica*, *P. mediterranea*, *Labidocera wollastoni* and *Anomalocera patersoni*, have on rare occasions been reported from the northern part of the Indian Ocean, and their presence there can be explained in the above way. Similarly a species that is normally to be found near the upper limit of the mid-water might ascend too far, and so get into the surface current and be carried westward; such a species is *Pleuromamma indica*, that has on a few occasions been recorded from the South Atlantic Ocean.

Another group of Holo-planktonic organisms that might be expected to show in their distribution a marked correlation with hydrographic conditions is the Scyphomedusae, as an example of which we may take the species *Periphylla hyacinthina*. This species is widely distributed in all three great oceans; in the Atlantic it has been taken from Greenland and the coast of Norway to the Antarctic, and its bathymetric range extends from some 50–2000 m. Stiasny (1934, 1937) has pointed out that young forms, in the *dodecabostrycha* stage, are usually found at a higher level than the older stages but have not been taken in the tropics in the upper levels except off Ascension and in the Gulf of Guinea. It seems probable that in the Atlantic the adult stage is a normal inhabitant of the North Atlantic Intermediate water, and is thus swept southwards; specimens have been taken off Cape Town at 3000 m. and further east off Kerguelen and beneath the West Wind Drift in depths ranging from 1000 to 3600 m., having in all probability been swept eastward in the branch of the North Atlantic Intermediate current that runs from the Atlantic to the Pacific Ocean. Small young stages occurring at a higher level will lie in the Sub-polar Intermediate water, and thus be swept northwards again, some of those in the Atlantic being carried eastward toward the African coast, where they may be caught up in the upwelling water that assists in the formation of the Benguela Current, and would thus be taken in the upper strata. In the Indian Ocean, as Stiasny (1937) points out, examples have been taken in an almost continuous series of Stations along the east African

coast from Zanzibar to Cape Guardafui and the Gulf of Aden, but rarely, if ever, in the Arabian Basin or the Maldive-Laccadive region, and he suggests that these medusae have been brought near the surface by upwelling water along the African coast and are then distributed by the Socotra Current, that sets northward (*vide* Matthews, 1926); as, however, these medusae in this area occur at depths ranging from 106 to 2000 m., with an optimum between 450 and 950 m., it seems more probable that they are carried northwards along the African coast in the Sub-polar Intermediate current. The extreme paucity of this species and of many others in the Arabian Basin is due to the character of the water in this area: we now know that in this region in the depths from about 500 to 1250 m. there is a marked deficiency in the oxygen content, and that the continental slopes and floor of the Gulf of Oman are an azoic area (*vide* Sewell, 1934); the extent to which this deficiency of oxygen affects the mid-water plankton is well illustrated in the accompanying table, in which I have given the actual numbers of individuals belonging to two common mid-water Calanoids from stations in the affected area and from neighbouring stations outside it.

Species.	Number of specimens obtained.	
Rhincalanus nasutus: Depth (m.).	*Affected area.* Stas. 61 A & C, 96.	*Unaffected area.* Stas. 76, 172 & 186.
0–200	13	671
200–600	942	1908
600–1000	0	2386
1000–1500	8	278
1500–2000	0	11
Eucalanus elongatus:		
0–200	0	304
200–600	258	6162
600–1000	137	567
1000–1500	144	351
1500–2000	1	0

In the greatest depths of the Southern Hemisphere the Antarctic Bottom Drift carries water from the South-polar region northwards, and in consequence out of some thirty-seven species of Calanoid-Copepoda that are definitely Antarctic six have been carried for varying distances into the Indian Ocean, one reaching the entrance to the Gulf of Oman, and seven have been carried into the Pacific Ocean. We have already seen that the northward flow of this bottom water is largely affected by the contours of the sea-floor, so that, though it can pass freely in the western side of the Atlantic, on the eastern side its passage is barred by the Walfisch Ridge; in this connection it is interesting to note that Stiasny (1931) has intimated that the abyssal fauna of the east and west Atlantic regions is not

the same, and that our ideas of the uniformity of the deep-sea fauna must be revised. Such a difference is only to be expected, since the bottom water on the west of the Mid Atlantic Ridge is Antarctic in origin, whereas that on the east side is Arctic or at least North Atlantic.

As regards the Nekton and the Benthos, the movements of these water masses must affect the distribution of their eggs or larval stages while these are planktonic; but the distance to which such forms can be carried by currents must depend on the rate of flow of the current and the length of the larval period. A study of the bottom topography, however, reveals the presence of a number of 'stepping stones', by means of which a species might be able in a series of successive generations to pass from one ocean to another.

The evidence appears to indicate that marine currents have a profound influence on the distribution of many of the groups of marine organisms, especially the Holo-plankton, and are sufficient to account for the frequency with which species are found to be cosmopolitan in habitat; but it seems equally clear that, in spite of the long period that has elapsed since the middle of the Tertiary Epoch, when the oceans assumed their present positions and connections, a uniformity of the fauna and flora has not yet been achieved either in the great depths or in the surface warm-water layer, nor will it ever be achieved so long as new species continue to make their appearance; furthermore, whether a species can become cosmopolitan seems to depend to a high degree on the ocean in which it has arisen, for it is difficult for warm-water surface species, that have arisen in the Atlantic Ocean, to get into the Pacific and on into the Indian Ocean, the only routes being in the North *via* the Arctic or in the south *via* the West Wind Drift, passage westward round Cape Horn being prevented by the eastwardly flowing current. Similarly, it is difficult for deep-living species that have originated in the Pacific or Indian Oceans to get into the Atlantic, since the Intermediate water from the Pacific, that flows eastward round Cape Horn, does not in all probability get beyond the Scotia Arc, while the Intermediate water flowing round the Cape of Good Hope passes from west to east, and so will prevent the passage of plankton in a westward direction.

Discussion.—

Dr. Anna B. Hastings considered the distribution of Antarctic and Subantarctic Cellularine Polyzoa. She showed that the distribution of the species is very closely related to hydrographic conditions, only 20 per cent. of Subantarctic and Antarctic species being common to the two regions as limited hydrographically by the Antarctic convergence.

A similar separation is noticeable, and usually even more marked, in the few other groups of animals for which data have been obtained.

The distribution of the genera of Antarctic Cellularine Polyzoa appears to point to eastern rather than western affinities, i.e. with the Australasian, Malayan and Japanese faunas rather than the American. This is also found in other groups, but not in the Antarctic Echinoderms, which have South American affinities (D. D. John, 1937). These tendencies are difficult to relate to present hydrological conditions, and are more probably due to inter-relations of the geological history of the region and the phylogeny of the groups.

Mr. J. R. NORMAN pointed out that fishes, being for the most part active swimmers, were not dependent upon the ocean currents for their distribution to nearly the same extent as the invertebrates already mentioned, although these currents undoubtedly play their part in transporting pelagic eggs and larval stages.

In the case of the coastal fishes, including not only the littoral forms but also those occurring at no great distance from the coasts in water down to a depth of about 500 metres, by far the most important hydrographical factor influencing their distribution is the temperature of the sea. By taking the mean annual surface isotherms of 6°, 12° and 20° C. respectively, it has proved possible to define a series of zones of distribution in the sea, each of which can be shown to be inhabited by more or less characteristic types of fishes. As an example, the distribution of the genus *Sardina* throughout the world lies fairly closely within the limits of the area bounded by the isotherms of 12° and 20° respectively. The isotherm of 12° runs roughly to the mouth of the English Channel, and it is just in this region that the warm-water forms such as the Pilchard, Anchovy and Red Mullet give way to colder-water types such as the Herring, Cod and Plaice. This also marks the southern limit of the Salmon and Trout as marine fishes. As another illustration of the part played by temperature in limiting distribution mention may be made of the islands of Tristan d'Acunha and St. Paul, in the South Atlantic and the southern part of the Indian Ocean respectively : although about 4,000 miles apart, these islands lie roughly on the same mean annual surface isotherm, and certain species of fish are found to be common to both, but to occur nowhere else. The current known as the Antarctic Drift runs direct from one island to the other, and this may well have been a factor assisting the spread of these fishes. Again, there are three species of Nototheniiform fishes common to the Patagonian-Falkland Islands region

and New Zealand—very many miles apart, but roughly on the same isotherm. There are about 90 species of fishes found in the Patagonian-Falkland Islands region, of which only three occur at South Georgia, a bare 800 miles away, but separated by the Antarctic Convergence, which corresponds closely to the isotherm of 6° C.

With regard to the oceanic fishes, the pelagic forms, although they seem to have on the whole a wider range than most coastal fishes, are still limited largely by temperature barriers. In the case of the abyssal forms, the contour of the sea floor may be an important factor in limiting their range, and it may be noted that the northern limit of the Macruridae is marked by the submarine ridge running from Scotland to Iceland and Greenland, which is less than 1,000 metres in depth. In the case of the bathypelagic fishes, it must be admitted that our knowledge of their distribution and the hydrographical factors involved is still far from complete, but a number of them appear to have a cosmopolitan range, and every fresh investigation increases this number. As many of them have a fairly extensive vertical range in the oceans, it is possible that they are able to negotiate barriers which would be effective in limiting the spread of coastal fishes, and that temperature may play a less important part in restricting the range of bathypelagic fishes.

Dr. Stanley Kemp thought there was one point, not hitherto mentioned, which should be considered in this discussion, namely, the comparative stability of the species which comprise the marine fauna. The chart of the distribution of land and water at the end of the Cretaceous period shows that the ancient sea of Tethys then extended from the Bay of Bengal and the Arabian Sea to the Atlantic, and that there was an open strait between North and South America. The Isthmus of Panama is thought to have been elevated during the Eocene, perhaps some 25 million years ago. It has, however, been found that a remarkable degree of resemblance still persists between the faunas on the two sides of the isthmus, and there are even some identical species. There is thus evidence that littoral forms, inhabiting what appears to be the most variable environment in the sea, can remain specifically constant over very long periods, and one would expect this stability to be still greater in the more uniform environment of the open ocean. In early Tertiary times hydrographic conditions must obviously have been altogether different from those of the present day, and it would be most interesting if our hydrographers, with the greatly improved knowledge they now possess, could be induced to speculate on the ocean currents which then prevailed.

Consideration of such facts as these—the stability of species and the vast hydrographic changes which must have occurred—in Dr. Kemp's opinion afforded the simplest explanation of the existence of certain bipolar species. The Euphausian *Thysanoessa gregaria* occurs in the Atlantic both in the north and in the south, but is entirely absent in the central Atlantic (even at depths where suitable temperatures are found) over a latitudinal distance of some 1,200 or 1,500 miles. It is not difficult to understand how the northern and southern stocks of this species might have been separated by the hydrographical changes which must have followed large-scale alterations in the distribution of land and water, and, as stated above, there is evidence that a species can remain constant for a very long period.

Such views as these appeared to have a bearing on the theories which Col. Sewell had brought forward in discussing the distribution of Copepoda. In contrast with most land and freshwater faunas, the marine fauna with its paucity of subspecies and varieties gave the impression of being ancient and long established, and if this is as true of the Copepoda as it seems to be of other groups any attempt to explain Copepod distribution in terms of existing ocean currents is likely to be fallacious.

As an instance of adaptation of plankton to hydrographic conditions Dr. Kemp cited the seasonal circulation of Antarctic macroplankton which had been described by Dr. N. A. Mackintosh (1937). All round the Antarctic continent the current system is the same—cold currents streaming to the north at both surface and bottom, and a warmer intermediate current flowing to the south. In spring and summer the rich phytoplankton, together with the zooplankton which feeds upon it, is carried steadily to the north, and in due course it would inevitably reach the Antarctic convergence, where the sudden rise in temperature would quickly prove fatal. Dr. Mackintosh has, however, found from series of observations made in the *Discovery II* that at least the more abundant species of the zooplankton sink in the autumn to greater depths, to as much as 750–1,000 m., and are thus carried back to the Antarctic in the south-going intermediate current. This remarkable circulation of the plankton is effected on a large scale, probably over some ten degrees of latitude, and it is difficult to resist the conclusion that it is a direct adaptation to the prevailing current system.

It has generally been thought that the deep-sea fauna shows a high degree of uniformity throughout the world, but it was becoming apparent that this was not universally true. Dr. Kemp had recently been studying extensive collections

of deep-water pelagic prawns belonging to the family Hoplophoridae, and he had found that one of the most abundant of them, usually known as *Acanthephyra purpurea*, had become differentiated in the different oceans, the separate species being distinguishable by apparently trivial but uniformly constant characters (Kemp, 1939, p. 568). Prof. Fage informed him that he had obtained almost identical results with the Lophogastrid Crustacea, and Dr. Kemp believed that Mr. Burkenroad in America was reaching similar conclusions with Decapods of the family Sergestidae.

Dr. Kemp gave a brief outline of the Atlantic distribution of the species belonging to the *Acanthephyra purpurea* group, pointing out that the central Atlantic between about 15° N. and 30° S. was exclusively occupied by two forms not found in any other part of the world. Mr. Norman, whom he had consulted, did not know of any pelagic fish with a similar range. Our present difficulty in reaching any general conclusions on the distribution of marine animals was that the data derived from different groups often showed a singular lack of correspondence. The discussion in his opinion had been useful, but in almost all groups much more detailed knowledge than we at present possess was needed.

Dr. G. P. Bidder noted that Dr. Burton had tentatively explained the transference of sponges from the Cape to the longitude of Australia by the eastward current, marked on the map, used by all speakers, like a railroad between the two positions. Although sponge larvae usually settle after 24 hours, some have been observed for two or three days; Dr. Burton suggested that in some circumstances free larval life may be longer.

Why trouble about the duration of larval life when sponge larvae can fix on a floating log and be carried to their destination as adults—with their children and grandchildren if the journey be long? We all know how the logs of Brazil wood used to make their lonely voyage across the shipless Atlantic.

Dr. Bidder regretted that he could supply few facts on the subject; but in the calcareous sponges, on which he worked for many years, gigantic specimens came from the bottoms of vessels moored long in harbour. At Naples *Leuconia aspera*, 15 cm. long, used to be found on ships in the old Porto Militare; and at Plymouth *Sycon ciliatum*, 18 cm. long, were gathered in quantity from a vessel which made a very long sojourn in Millbay Dock.

Even if the inordinately long cylinder were broken off in the sea-voyage, sufficient of the base would remain to populate a continent.

Professor W. Garstang remarked that the duration of larval life is important in matters of dispersal, and suggested

contrasting the ranges of species with long-lived larvae and short-lived larvae.

References.

Alcock, A. 1898. A summary of the deep-sea zoological work of the Royal Indian Marine Survey ship *Investigator* from 1884 to 1897. *Sci. Mem. Med. Officers Army India*, part xiii.

Apstein, C. 1905. Salpen der deutsch Tiefsee Expedition. *Wiss. Ergebn. Valdivia*, xii.

—— 1906. Die Salpen der Deutsch-Sudpolar Expedition, 1901–1903. *Wiss. Ergebn. deutsch. Sudpolar-Exped.* ix, Zoologie, 1.

Barnard, K. H. 1936. Isopods collected by the R.I.M.S. *Investigator*. *Rec. Ind. Mus.* xxxviii, pt. 2, p. 147.

—— 1937. Amphipoda. The John Murray Expedition, 1933–34. *Sci. Reports*, iv, no. 6.

Bedot, M. 1909. La Faune eupelagique (Holoplancton) de la Baie d'Amboine. *Rev. suisse Zool.* xvii, pt. 1.

Børgesen, F. 1934. Some marine algae from the northern part of the Arabian Sea, with remarks on their geographical distribution. *Kongl. Danske vidensk. Selsk. Biol. Meddelelser*, xi, no. 6.

Burton, M. 1930. Norwegian sponges from the Norman Collection. *Proc. Zool. Soc. London*, pt. 1.

—— 1932. Sponges. *Discovery Reports*, vi, p. 237.

—— 1934. Sponges. Great Barrier Reef Expedition, 1928–29. *Sci. Reports*, iv, no. 14.

Calman, W. T. 1938. Crustacea : Caridea. The John Murray Expedition, 1933–34. *Sci. Reports*, vi, no. 4.

Clark, A. H. 1912. The Crinoids of the Indian Ocean. Echinoderma of the Indian Museum, pt. vii. Publ. by the Trustees of the Indian Museum.

—— 1913. The Atlantic Ocean biologically an inland sea. *Internat. Rev. Hydrob. Hydrog.* vi.

—— 1936. Crinoidea. John Murray Expedition, 1933–34. *Sci. Reports*, iv, no. 4.

Cleve, P. T. 1900. The seasonal distribution of Atlantic plankton organisms. Göteborg.

Clowes, A. J. 1933. Influence of the Pacific on the circulation in the south-west Atlantic Ocean. *Nature*, cxxxi, p. 189.

—— & Deacon, G. E. R. 1935. The deep-water circulation of the Indian Ocean. *Nature*, cxxxvi, p. 936.

Crossland, C. 1928. Notes on the ecology of the reef builders of Tahiti. *Proc. Zool. Soc. London*, pt. 2, p. 717.

Damas, D., & Koefoed, E. 1907. Le plankton de la mer du Grönland ; in Duc d' Orléans, Croisière océan. Mer du Grönl. 1905, Rés. Sci., Bruxelles.

Deacon, G. E. R. 1937. The hydrology of the Southern Ocean. *Discovery Reports*, xv, p. 3.

Defant, A. 1930. Die Ozeanische Zirkulation. Congreso Internacional di Oceanografia, Hidrografia marina e Hidrologia continental, Sevilla, 1929, i.

Ekman, S. 1935. Tiergeographie des Meeres. Leipsig.

Farran, G. P., & Calman, W. T. 1928. Animals of the sea-floor, in Science of the Sea, 2nd edition, chapter vii.

Fauvel, P. 1932. Annelida Polychaeta of the Indian Museum, Calcutta. *Mem. Ind. Mus.* xii, no. 1.

Fischer-Piette, E. 1936. Études sur la biogeographie intercotidale des deux rives de la Manche. *Journ. Linn. Soc. London*, xl, Zoology, no. 270.

Fox, H. Munro. 1929. The Cambridge Expedition to the Suez Canal, 1924. Summary of results. *Trans. Zool. Soc. London*, xxii.

Fraser, F. C. 1936. On the development and distribution of the young stages of the Kroll (*Euphausia superba*). *Discovery Reports*, xiv.

Giesbrecht, W. 1892. Pelagischer Copepoden. Fauna und Flora des Golfes von Neapel, xix.

Gregory, J. W. 1929. The geological history of the Atlantic Ocean. *Quart. Journ. Geol. Soc. London*, lxxxv.

Gurney, R. 1927. Report on the Crustacea: Copepoda and Cladocera of the plankton. Cambridge Expedition to the Suez Canal, 1924. *Trans. Zool. Soc. London*, xxii.

Haeker, V. 1908. Tiefsee-Radiolarien. *Wiss. Ergebn. Valdivia*, xiv.

Hardy, A. C. 1923. Notes on the Atlantic plankton taken off the east coast of England in 1921 and 1922. *Publ. Circ. Cons. Explor. Mer.* no. 80.

—— 1936. Plankton ecology and the hypothesis of animal exclusion. *Proc. Linn. Soc. London*, 1935–36, part 2, p. 64.

—— & Gunther, E. R. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926–27. *Discovery Reports*, xi.

Hart, T. J. 1937. *Rhizosolenia curvata* Zacharias, an indicator species in the Southern Ocean. *Discovery Reports*, xvi.

Holland, Sir T. H. 1937. The permanence of oceanic basins and continental masses. Huxley Memorial Lecture. Macmillan & Co., London.

Isaac, W. E. 1937. South African coastal waters in relation to ocean currents. *Geogr. Rev.* xxvii.

John, D. D. 1937. Antarctic comatulids. *Proc. Linn. Soc. Lond.*, 149 Sess., p. 85.

Kemp, S. W. 1910. The Decapod Natantia of the coasts of Ireland. *Fisheries, Ireland, Sci. Invest.* 1908, no. 1.

—— 1938. Oceanography and the fluctuations in the abundance of marine animals. Presidential Address, Section D: British Association Report, Cambridge.

—— 1939. On *Acanthephyra purpurea* and its allies (Crustacea Decapoda: Hoplophoridae). *Ann. Mag. Nat. Hist.* (ser. 11) iv.

Lehnhofer, K. 1926. Copepoda: Copilia. *Wiss. Ergebn. Valdivia*, xxiii, pt. 3.

Lysholm, B., & Nordgaard, O. 1921. Copepoda collected on the cruise of the M./S. *Armauer Hansen* in the North Atlantic, 1913. *Bergens Mus. Aarb.* 1918–19, Naturvidenskabelig raekke, nr. 2.

Mackintosh, N. A. 1937. The seasonal circulation of Antarctic Macroplankton. *Discovery Reports*, xvi, p. 365.

Matthews, D. J. 1926. The Percy Sladen Trust Expedition to the Indian Ocean in 1905: physical oceanography. *Trans. Linn. Soc. London*, ser. 2, Zoology, xix, pt. 1.

Meisenheimer, J. 1905. Pteropoda. *Wiss. Ergebn. Valdivia*, ix.

Metcalf, M. M. 1918. The Salpidae: a taxonomic study. *U.S. Nat. Mus., Bull.* 100.

Meyer, K. 1933. Die geographische Verbreitung der tripyleen Radiolarien des Südatlantischen Ozeans. *Wiss. Ergebn. Meteor.* 1925–27, xii, no. 1.

Mohamed, A. D. 1940. Oceanographical and chemical researches in the Indian Ocean and Red Sea. The John Murray Expedition, 1933–34. *Sci. Reports*, ii.

MONRO, C. C. A. 1937. Polychaeta. The John Murray Expedition, 1933–34. *Sci. Reports*, IV.

MOORE, H. B., & KITCHING, J. A. 1939. The biology of *Chthamalus stellatus* (Poli). *Journ. Mar. Biol. Ass. U.K.* XXIII.

MURRAY, G. 1893. Phycological Memoirs, pt. ii.

NORMAN, J. R. 1939. Fishes. The John Murray Expedition, 1933–34. *Sci. Reports*, VII.

PARKER, H. W. 1939. Turtles stranded on the British coast. *Proc. Linn. Soc. London*, 1938–39, pt. 2.

PELSENEER, P. 1887. Pteropoda. *Sci. Results of the Voyage of the Challenger, Zoology*, XIX.

PESTA, O. 1920. Die Planctoncopepoden der Adria. *Zool. Jahrb.*, Abt. Syst. LXIII.

PETTERSSON, O. 1927. Aperçu d'orientation vers la conception actuelle de la circulation océanique dans l'atlantique. *Svenska hydrogr.-biol. Komm. Skr. Hydrog.* V.

RAMADAN, M. M. 1938*a*. Crustacea : Penaeidae. The John Murray Expedition, 1933–34. *Sci. Reports*, V.

—— 1938*b*. The Astacura and Palinura. The John Murray Expedition, 1933–34. *Sci. Reports*, V.

REID, D. M. 1935. The range of the sea urchin, *Echinus esculentus*. *Journ. Anim. Ecol.* IV.

RIEL, P. M. VAN. 1934. The bottom configuration in relation to the flow of the bottom water. The Snellius Expedition : oceanographic results, II, part 2, chapter ii.

—— 1938. The influence of the bottom configuration on the properties of the sea-water in the abyssal layers. *Comptes-rend. Congres Internat. Geographie, Amsterdam*, II.

ROBSON, G. C. 1924. On the Cephalopoda obtained in South African waters by Dr. J. D. F. Gilchrist in 1920–21. *Proc. Zool. Soc. London*, XXXIX.

RUSSELL, F. S. 1930. Do oceanic plankton animals lose themselves ? *Nature*, January 4, 1930.

—— 1935*a*. On the value of certain planktonic animals as indicators of water movements in the English Channel and North Sea. *Journ. Mar. Biol. Ass. U.K.* XX.

—— 1935*b*. A review of some aspects of zooplankton research. *Rapp. Cons. Explor. Mer*, XCV.

SCHMAUS, P. H., & LEHNHOFER, K. 1927. Copepoda 4 ; *Rhincalanus* Dana, 1852. Systematik und Verbreitung der Gattung. *Wiss. Ergebn. Valdivia*, XXII.

SCHMIDT, J. 1932. Danish eel investigations during 25 years (1905–1930. (English translation from Dana's ' Togt Omkring Jorden ', 1928–1930.) Published by the Carlsberg Foundation.

SCHOTT, G. 1926. Geographie des Atlantischen Ozeans. Hamburg.

—— 1928. Die Wasserbewegungen im Gebiet der Gibraltarstrasse. *Journ. Cons. Internat. Explor. Mer*, III, no. 2.

—— 1935. Geographie des Indischen und Stillen Ozeans. Hamburg.

SEWELL, R. B. S. 1925. Geographic and oceanographic research in Indian waters : Pt. 1. The geography of the Andaman Sea basin. *Mem. Roy. Asiatic Soc. Bengal*, IX.

—— 1932. Geographic and oceanographic research in Indian waters : Pt. 6. Temperature and salinity of the deeper waters of the Bay of Bengal and Andaman Sea. *Mem. Roy. Asiatic Soc. Bengal*, IX.

—— 1934. The John Murray Expedition to the Arabian Sea. *Nature* CXXXIII, p. 86.

—— 1940. Copepoda Harpacticoida. John Murray Expedition, 1933–34. *Sci. Reports*, VII.

STEPHENSON, T. A., and DU TOIT, C. A. 1937. The South African intertidal zone and its relation to ocean currents. *Trans. Roy. Soc. S. Africa*, XXIV.

STEUER, A. 1928. Zur faunistischen Charakterisierung des Südafrikanischen Mischgebietes. *Internat. Rev. Hydrobiol.* XX.

—— 1931. Grössen- und Formvariation d. Planktoncopepoden. *Sitz-ber. Akad. Wiss. Wien*, Math.-Naturw. Kl. 140.

—— 1933. Zur planmässigen Erforschung der geographischen Verbreitung des Haliplanktons besonders der Copepoden. *Zoogeographica*, I, pt. 3.

STIASNY, G. 1931. Über das Alter u. d. Herkunft d. Tiefseefauna. *Verhandl. d. Deutsch (Zool. Anz. Supplbd.* v.).

—— 1934. Scyphomedusae. *Discovery Reports*, VIII.

—— 1937. Scyphomedusae. The John Murray Expedition, 1933–34. *Sci. Reports*, IV. no. 7.

STUBBINGS, H. G. 1936. Cirripedia. The John Murray Expedition, 1933–34. *Sci. Reports*, IV, no. 1.

SVEDELIUS, N. 1906. Ecological and systematic studies of the Ceylon species of *Caulerpa*. *Rep. Ceylon. Mar. Biol. Lab.* no. 4.

SVERDRUP, H. U. 1931. The origin of the deep water of the Pacific Ocean as indicated by the oceanographic work of the *Carnegie*. *Gerlands Beitr. Geophys.* XXIX, p. 95.

TATTERSALL, W. M. 1939. The Euphausiacea and Mysidacea of the John Murray Expedition to the Indian Ocean. The John Murray Expedition, 1933–34. *Sci. Reports*, V. no. 8.

THOMPSON, E. F. 1939. Chemical and physical investigations; the exchange of water between the Red Sea and the Gulf of Aden over the 'Sill'. The John Murray Expedition, 1933–34. *Sci. Reports*, II, no. 4.

THOMSEN, H. 1933. The circulation of the Indian Ocean. *Journ. Cons. int. Explor. Mer.* VIII, p. 73.

UMBGROVE, J. H. F. 1938. On the time of origin of the submarine relief in the East Indies. *Comptes-rend. Congres Internat. de Geographie, Amsterdam*, II, sect. ii *b*.

VAILLAUX, C. 1938. La circulation de profondeur dans les grands oceans. *Comptes-rend. Congres Internat. de Geographie, Amsterdam*, II, part 2.

VAUGHAN, T. WAYLAND. 1919. Corals and the formation of coral reefs. Smithsonian Report for 1917, p. 189.

WISEMAN, J. D. H., and SEWELL, R. B. S. 1937. The floor of the Arabian Sea. *Geol. Mag. Lond.* LXXIV.

WÜST, G. 1928. Der Ursprung der atlantischen Tiefenwässer. *Zeitschr. Ges. Erdk. Berlin*, 1828–1928. Berlin.

—— 1934. Anzeichen von Beziehungen zwischen Bodenstrom und Relief in der Tiefsee des Indischen Ozeans. *Naturwissenschaften*, 1934, 22 Jahrg. Heft. 16 (verlag von Julius Springer, Berlin).

—— 1936. Deep circulation in the expanse of the North Atlantic Ocean. *Hydrogr. Rev.* XIII, no. 2 (reproduced from *Naturwissenschaften*, Berlin).

PROCEEDINGS OF THE GENERAL MEETING
9 May 1940

Mr. J. Ramsbottom, O.B.E., M.A., Dr.Sc., President, in the Chair

The Proceedings of the General Meeting held on Thursday, 25 April 1940, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted :—Richard Clements.

Certificates of recommendation of the following candidates for Fellowship were read :—For the first time, in favour of James Insch and Colin Fraser Symington.

The following candidates, whose names were read for the third time, were balloted for and elected Fellows :—Donald Albert Coult, M.Sc., Francis Charles Fraser, D.Sc., and Kailas Nath Kaul, M.Sc.

The following candidates, whose names were read for the third time, were balloted for and elected Foreign Members :—Dr. Thomas Barbour and Prof. August Adriaan Pulle.

Capt. J. Guy Dollman exhibited and gave an account of (*a*) 'Two skulls of the Pigmy Hippopotamus presented to the British Museum (Natural History) by I. R. P. Heslop, Esq., from Southern Nigeria'; (*b*) An abnormal pig's jaw from New Zealand.

Abstract.—

Captain Dollman, in referring to his exhibit of two skulls of the Pygmy Hippopotamus (*Choeropsis liberiensis*) from Southern Nigeria, made the following remarks :—

In 1938, through the good offices of the Society for the Preservation of the Fauna of the Empire, I received an account, accompanied by photographs, sent home by Mr. I. R. P. Heslop, of two skulls of the Pygmy Hippopotamus from the Owerri and Warri Provinces, Southern Nigeria. From this evidence it was obvious that the rumours one had heard previously of the occurrence of the Pygmy Hippopotamus in Nigeria were correct, and a letter of mine, published in

The Times of July 22nd, 1938, brought this interesting fact to public notice.

The Natural History Museum has now received as a donation from Mr. Heslop the two skulls which were referred to in this letter. They represent adult and sub-adult specimens of the Pygmy Hippopotamus, and thus the extension of the range already noted is now conclusively proved. It was formerly held that this species was confined in its distribution to a comparatively small area of West Africa, i.e. Sierra Leone, Liberia and the French Ivory Coast, and, therefore, its occurrence as far east as Southern Nigeria is a fact of outstanding importance. It is possible that the range of this animal may be even still greater than is at present known and may extend into French Equatorial Africa.

Mr. Heslop is to be congratulated on this very interesting discovery.

Captain Dollman also referred to an abnormal pig's jaw from New Zealand, brought home by Sir Lionel Fletcher. The tusks in the lower jaw have grown backwards and downwards so as to pierce the alveolar border in the middle of the row of cheek teeth. To such an extent has this abnormality developed that in the right tusk a complete circle is nearly formed. Sir Frank Colyer has told me, said Captain Dollman, that abnormalities of this type are sometimes produced by the natives destroying the upper tusks so that the lower ones, having no opposition, tend to grow round in a circle.

Captain Dollman pointed out that such abnormalities in dentition were by no means rare amongst rabbits and rats, in which the loss of either the upper or lower incisors allows the unrestricted growth of the opposite incisors, a complete circle thus being frequently formed.

Dr. G. P. Bidder asked if the pigmy Rhinoceros fossil in Malta was related : Capt. Dollman replied—not generically.

Mr. D. J. Scourfield, I.S.O., gave an account of his paper, ' Two new and nearly complete specimens of young stages of the Devonian fossil Crustacean *Lepidocaris rhyniensis* '. [Printed in full, p. 290.]

Mr. S. Savage gave an account of his ' Synopsis of the annotations by Linnaeus and contemporaries in his library of printed books '. [Printed as ' Catalogue of Manuscripts ', Part III.]

The annotations by Linnaeus, the younger Linnaeus and other contemporaries in the printed books in the Linnaean library are indicated under classified headings.

Professor F. E. Weiss congratulated Mr. Savage on the completion of a good and useful piece of work. It would

not only be of value to the Society as a record of annotations in Linnaeus' library, but would also be of use to British and foreign investigators who may have to deal with the identification of plants and to whom all Linnaeus's records, even annotations, are of importance.

Miss M. S. Campbell and Mr. A. J. Wilmott gave an account of 'A botanical expedition to Lewis and Harris', which was illustrated with coloured photographs (Ciné film and lantern).

Dr. G. B. Bidder, Mr. A. H. G. Alston, Mr. H. W. Pugsley, and the President added comments; Mr. Wilmott replied.

The following papers were read in title :—

'Two new Chrysophycean Flagellates.' By Dr. W. F. Jane, F.L.S. [Printed in full, p. 298].

'On the biology of two *Latrodectus* spiders in Palestine.' By A. Shulov. (Communicated by Capt. C. Diver, F.L.S.) Printed in full, p. 309].

'Studies in *Aquilegia*. By Dr. M. Skalinska. (Communicated by the Botanical Secretary.) [Printed in full, p. 328].

'On the larvae of certain Crustacea Macrura, mainly from Bermuda.' By Dr. Robert Gurney, F.L.S., and Dr. Marie V. Lebour.

'The identification of Coniferous woods by their microscopic structure.' By E. W. J. Phillips. (Communicated by Prof. V. H. Blackman, F.R.S., F.L.S.)

'Contributions towards the Fungus Flora of Uganda.—III. Some Uganda Ascomycetes.' By C. G. Hansford F.L.S.

'Percy Sladen Expedition to Lake Titicaca, 1937. Scientific Reports.—VIII. Crustacea: Anostraca and Conchostraca.' By J. P. Harding, Ph.D. IX.—Charophyta. By G. O. Allen, M.A. X.—Algae. By T. G. Tutin, M.A. (Communicated by Prof. J. Stanley Gardiner, M.A., F.R.S., F.L.S.)

The President announced that his Presidential Address, to be given at the Anniversary Meeting on Friday, 24 May 1940, will be entitled 'On a collection of Dillenian drawings'.

TWO NEW AND NEARLY COMPLETE SPECIMENS OF YOUNG STAGES OF THE DEVONIAN FOSSIL CRUSTACEAN LEPIDOCARIS RHYNIENSIS.

By D. J. Scourfield, I.S.O., F.L.S., F.R.M.S.

In my paper (Scourfield, 1926) on the little fossil crustacean *Lepidocaris rhyniensis* from the Rhynie Chert (Middle Old Red Sandstone=Middle Devonian) I was able to give illustrations of several stages in the development of the animal, commencing with a form one-eightieth of an inch long and with a body of only four somites. All these specimens were, however, very incomplete, and it seems advisable therefore to put on record the subsequent discovery of two specimens of young stages both of which are in a much more perfect state of preservation.

As will be seen from the accompanying figures 1 and 2 the specimens are very nearly at the same stage of development, probably only separated by a single moult, for in one case (fig. 2) there appear to be eight somites and in the other nine. They closely correspond in age therefore to the specimens shown in figures 38, 39 and 40 of the paper already mentioned. They are both about one-fortieth of an inch in length, and consequently just twice the length of the youngest form so far found, and with about double the number of somites. They are, however, still in quite an early stage of development, for the adult had nineteen somites and was about one-eighth of an inch long.

Description of the specimens.

Body segments (*somites*).—As was to have been anticipated, the first body segment, comprising the head and first pair of thoracic limbs, in these young specimens was much larger in proportion to the other segments than in the adult, measuring nearly two-fifths, as against about one-fifth, of the whole body length. The frontal margin, well preserved in specimen 1 though not very clear in specimen 2, appears to have been nearly straight. This is the first time that such a definite outline of the front of the head, as seen from above, has been obtained. Whether this rather square form continued or became more rounded in the adult, as was assumed in the reconstruction in the original paper, is still unknown. By focussing down a little from the sharpest image of this front edge two shallow depressions come into view, one on either side. The suggestion may be made that these represent the position of a pair of 'frontal organs' corresponding to those occurring in the young of *Chirocephalus* and other Branchiopoda.

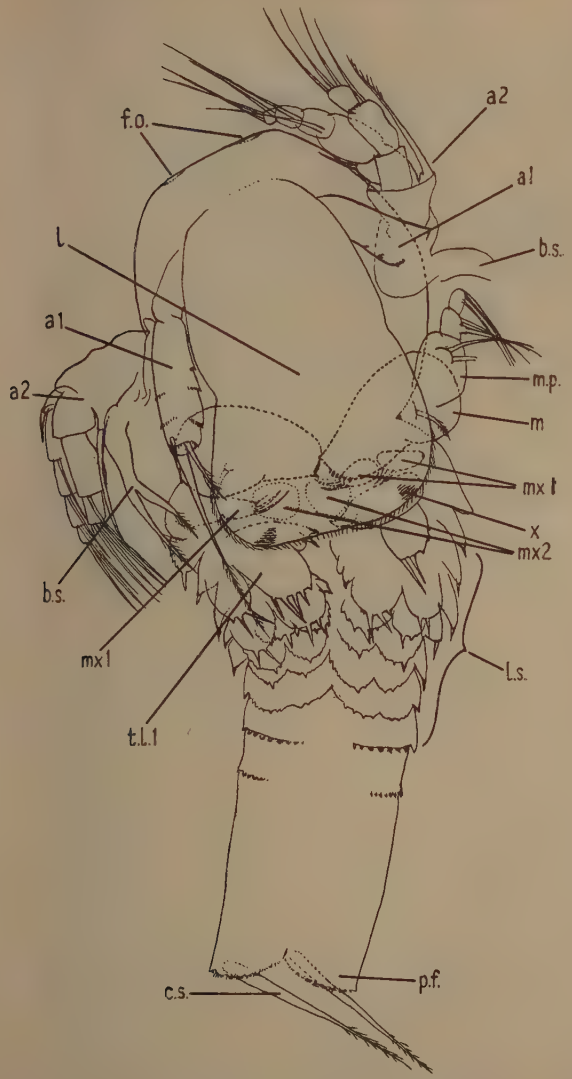


FIG. 1.—Young specimen (No. 1) of *Lepidocaris rhyniensis* with nine somites. Ventral view. × 200. (This specimen was found by the late Mr. S. Hirst when searching for arachnid remains in the Rhynie Chert. Registered number in British Musem (Nat. Hist.) In.38486.)

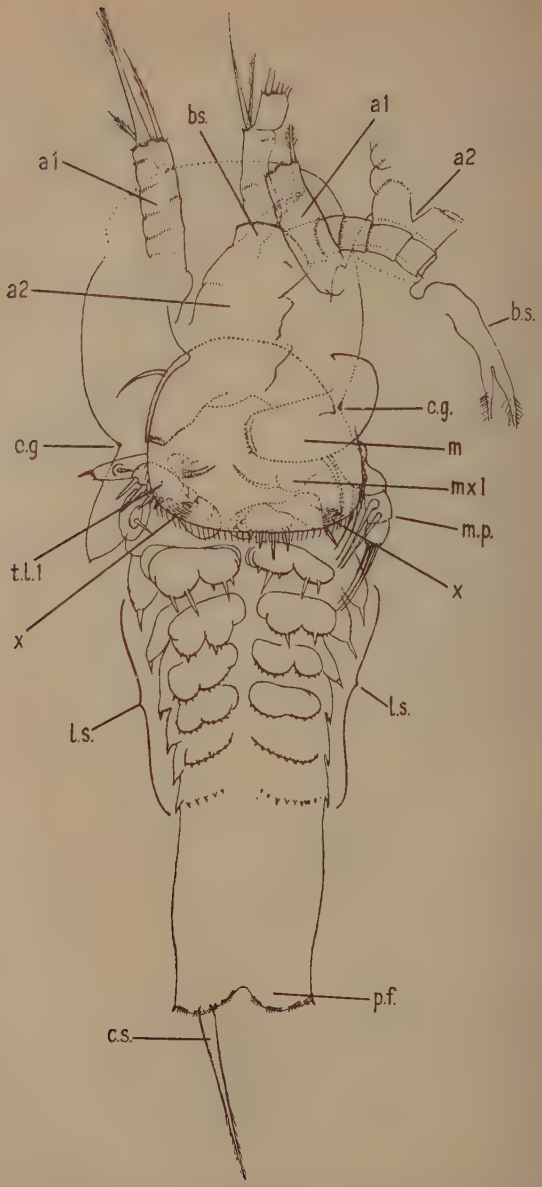


FIG. 2.—Young specimen (No. 2) of *L. rhyniensis* with eight somites. Ventral view. × 200. (This specimen was found during the 'further search for animal remains in the Rhynie Chert', for which a grant was made by the Royal Society from the Government Grant Fund. Registered number in British Museum (Nat. Hist.) In.38487.)

A striking feature, shown by both specimens, is the deep bay on either side in the posterior part of this first somite. This evidently corresponds in position to the so-called cervical (mandibular) groove, which is no doubt present on the back, and shows that the groove is continued down the sides of the somite for a greater distance than might have been expected.

Another noticeable feature of the first somite is the enormous labrum. Specimen 1 shows this practically in its entirety, and the posterior portion is also well shown in specimen 2. It will be seen from the figures that it was somewhat contracted in the middle of its length, that its broad posterior margin was almost straight, and that this margin and the sides for some distance up were fringed with short hairs. A peculiar structure occurs near each of the two posterior corners of the labrum. It consists of a group of nearly parallel short vermiform lines, which do not seem to be setae, but may be a series of minute tubes in the structure of the chitin. They occur in both specimens, but are more noticeable in number 2 (*x*).

The somites following the first, but in front of the caudal segment, are much shorter than broad, and show a fairly steady diminution in both length and breadth from the front backwards. Their dorsal posterior margins are notched or minutely toothed (see fig. 3). The anterior members of the series show well-developed lateral scales, and there is some indication of such scales developing even on the posterior ones. It seems clear from the present specimens, particularly no. 2, that these lateral scales are not developed from the trunk limbs but from the pleurae of the somites, thus confirming previous conclusions on the subject. This is a point of much importance in discussions on the interrelationships of the various types of Crustacea (see Garstang and Gurney, 1938).

The caudal segment is about the same width as the preceding segment, but it is very much longer, being rather more than half the length of the first segment and therefore the second longest of the whole series. It is not quite cylindrical, as there is a very slight swelling near the middle. Posteriorly it is bifurcated, or, at least, deeply notched, and bordered by little groups of minute short spines or fringed scales. Each half of the bifurcation carries a characteristic seta. In the original paper on *Lepidocaris* these parts were alluded to as the 'primary furca' and 'conical setae' respectively, and it was shown that they persist into the adult state, even after a much larger 'secondary furca', of which there is as yet no trace in the present specimens, had developed.

Antennules.—These organs have not been previously seen in such young specimens, and they differ materially from the adult form. Specimen 1 shows one antennule in a practically

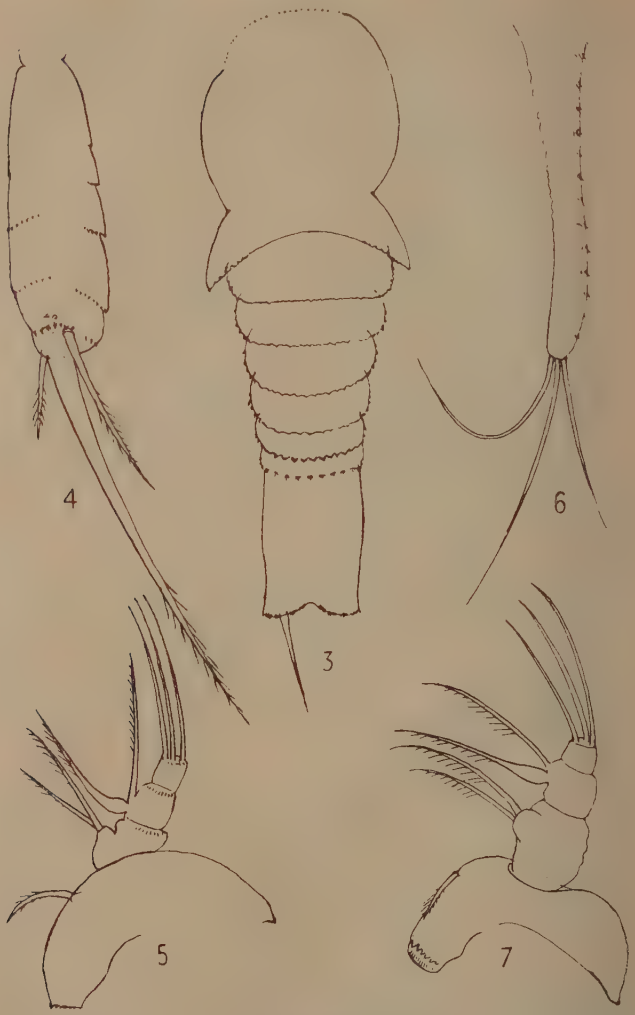


Fig. 3.—Same specimen as fig. 2, showing dorsal side as seen by focussing through from the ventral side. × 140.
Fig. 4.—Antennule of specimen 1. × 400.
Fig. 5.—Mandible ' palp ' of specimen 2. × 250.
Fig. 6.—Antennule of young of *Chirocephalus diaphanus*. × 150.
Fig. 7.—Mandible ' palp ' of *Chirocephalus diaphanus*. × 150.

perfect condition, and one nearly as good is to be seen in specimen 2, while partial remains of the other member of each pair can be seen. At this stage (fig. 4) they appear to have consisted of a single rather thick segment, about three times as long as broad, with several partial rings of minute teeth and with three terminal setae. Two of the latter, one originating a little way back from the tip of the antennule, were nearly equal, much shorter than the antennule, and of normal appearance. The third was of a very striking appearance, being much longer than the antennule and exceptionally massive towards the base. No evidence of the presence of the so-called olfactory setae on the antennule has been found in these specimens. In contrast to the foregoing it may be recalled that in the adult the antennules became elongated and three-segmented, and that the only setae present were some exceedingly delicate ones at the tip, probably of the olfactory type.

It is interesting to compare these larval antennules with those of the young in such a form as *Chirocephalus* (fig. 6), where, in the first stages at any rate, there are also three prominent setae at the tip of the one-segmented antennule and no olfactory setae. Later on olfactory setae appear near the tip and the three terminal setae become much reduced, relatively if not actually.

Antennae.—These are very well shown in specimen 1, but are only fragmentary in specimen 2. They evidently consisted of a large protopodite of two (? three) segments and two branches, the endopodite of three and the exopodite of five segments. From the base of the protopodite arises a very large bifid seta (masticatory process) and from its distal segment a strong simple seta. Both of these can be matched exactly in young forms of *Chirocephalus* and other branchiopods. The segments of the branches mostly give rise to one seta, but the terminal segments to three each. These details of the antennae confirm and expand somewhat the information available when the original paper was written.

Mandibles.—Both specimens show well developed mandibles of typical branchiopod character with large 'palps' still attached to them. In each of figures 1 and 2 the palp on one of the mandibles has been omitted so as not to complicate the drawing too much, but one of them has been given separately in fig. 5. This new evidence as to the structure of the palps fully confirms that given in the original paper (p. 180, figs. 46 and 47).

In an address to the Essex Field Club (Scourfield, 1930) I pointed out the extraordinary similarity of the mandibular palps of young *Lepidocaris rhyniensis* to those of the young of the modern fairy shrimp *Chirocephalus diaphanus*. Not

only are there the same three segments, each with the same number of setae, but the setae themselves are of exactly the same pattern. In each case the three terminal setae appear not to be feathered whilst the others are feathered only on one and the same side. More remarkable still the proximal seta on the middle segment has a bulbous base in each case. As there seems no possibility that *Chirocephalus* is descended from *Lepidocaris* it follows that both must have inherited this identical form of palp from a still more remote common ancestor. Such persistence of a particular structure in all its minute details through hundreds of millions of years, notwithstanding its organic association with other structures which during that time must have undergone profound modifications, is surely a fact of much significance and one not to be forgotten in discussions on the problems of inheritance and evolution. Probably it may be a point of some importance in this connection that, in these cases, the palp is only a larval structure which disappears altogether in the adult stage.

Maxillules.—These are present in both specimens, but the exact details are not very easy to make out. In specimen 1, however, they certainly consist of two lobes (most clearly seen in the left maxillule) which must represent the endopodite and exopodite of an originally biramous appendage. The inner lobe is evidently the usual small branchiopod maxillule with only a few setae. The outer lobe, which bears two setae, may be interpreted in two ways. It may, of course, be simply the vestigial exopodite destined to disappear in the adult, or it may represent in this particular case an early stage of the male clasper. I would like to think that the latter is the true interpretation, as it would prove the correctness of my belief that the male claspers in *Lepidocaris* originated from the maxillules, a view about which some doubt has been expressed (see Eriksson, 1934). Unfortunately the structure in this specimen is not sufficiently detailed to settle the matter.

Maxillae.—Just under and very slightly posterior to the maxillules can be seen, in specimen 1, a pair of more or less rounded structures which from their position I think must be the rudiments of a pair of maxillae. In my original paper a drawing was given (fig. 32) of a specimen in which there appeared to be traces of a pair of very rudimentary maxillae, and subsequently Prof. Cannon (1933) published figures of other specimens in which these vestigial maxillae were plainly visible. Whether, therefore, the rounded structures alluded to represent maxillae or not, it is now certain that rudimentary maxillae did occur in *Lepidocaris*, at any rate up to a comparatively late stage of development.

Trunk Limbs.—The first one or two pairs of trunk limbs in both specimens are fairly well developed, but are considerably simpler and much more definitely biramous than in the adult. The right first trunk limb of specimen 1 shows this most clearly *. The exopodite, instead of being small and projecting laterally as in the adult, is nearly as large as the endopodite and parallel with it and the strong pectinate spines which fringe the ' palmate apical lobe ' of the endopodite in the adult are here only represented by four or five ordinary spines. Some at any rate of the endites are already present though in a rudimentary condition.

The remaining pairs of trunk limbs show less and less structure as we proceed backwards until they are only represented by narrow transverse lobes with the merest indication of division into two halves by a slight median notch. Since in the adult the first three pairs of trunk limbs are of a distinctly foliaceous pattern, while the others are copepodoid in character, these young specimens show clearly how the two types can be derived from the same initial rudiments which themselves must be regarded as fundamentally biramous. The evidence from *Lepidocaris* therefore appears to support the view that the primitive crustacean limb was biramous rather than foliaceous. (For various opinions on this subject see Borradaile (1926) and Calman (1926).)

Discussion.—

Dr. J. P. Harding congratulated Mr. Scourfield on the results of his patient and painstaking investigations. In 1926 Mr. Scourfield had shown that the anterior trunk limbs of *Lepidocaris* were foliaceous, while the posterior ones were biramous. The relationships between the two types of crustacean limb had long been one of the central problems in discussions on the evolution of the Crustacea. The two rami of the biramous limbs of *Lepidocaris* were obviously homologous with the flabellum and the distal endite of the foliaceous limbs in front. It was now easy to see how one type of limb had been derived from the other; but it was still difficult to decide which was the more primitive. As the possession of foliaceous appendages is characteristic of the lower orders of known Crustacea it was generally assumed that this was the primitive type of crustacean appendage. Dr. Calman had, however, pointed out that it was usual for the more posterior of a series of limbs to be the more primitive, and that it was likely that *Lepidocaris* had primitively biramous appendages of which the more anterior had become foliaceous by

* Curiously enough in this specimen the endopodite of the left first trunk limb appears to be missing.

specialization. This point of view is very strongly supported by the work which Mr. Scourfield has just communicated, for he now finds that all the trunk limbs of *Lepidocaris*, including the foliaceous anterior pairs, are distinctly biramous in their early stages of development.

References.

Borradaile, L. A. 1926. On the primitive phyllopodium. *Ann. & Mag. Nat. Hist.* (9) xviii, pp. 16–18.

Calman, W. T. 1926. The Rhynie Crustacean. *Nature*, cxviii, pp. 89–90.

Cannon, H. G. 1933. On the feeding mechanism of the Branchiopoda. *Phil. Trans.* B, ccxxii, pp. 267–352.

Eriksson, S. 1934. Studien über die Fangapparate der Branchiopoden. *Zool. Bidrag Uppsala*, xv, pp. 23–287.

Garstang, W., & Gurney, R. 1938. The descent of Crustacea from Trilobites, and their larval relations. Article in ' Evolution, Essays presented to E. S. Goodrich ', pp. 271–286.

Scourfield, D. J. 1926. On a new type of Crustacean from the Old Red Sandstone. *Phil. Trans.* B, ccxiv, pp. 153–187.

—— 1930. Some biological problems as illustrated by the Entomostraca. *Essex Naturalist*, xxiii, pp. 2–18

Explanation of lettering of text-figures.

a 1. Antenna of first pair (antennule).
a 2. Antenna of second pair (antenna).
b.s. Bifid seta (masticatory process) of antenna.
c.g. Cervical (mandibular) groove—lateral prolongation.
c.s. Conical seta of primary furca.
f.o. Frontal organ ?.
l. Labrum.
l.s. Lateral scales.
m. Mandible.
m.p. Mandible palp.
mx 1. Maxillula.
mx 2. Maxilla.
p.f. Primary caudal furca.
t.l. Trunk limb.
x. Problematical structure on labrum.

TWO NEW CHRYSOPHYCEAN FLAGELLATES—CYCLONEXIS ERINUS AND SYNOCHROMONAS ELAEOCHRUS.

By F. W. Jane, Ph.D., F.L.S.

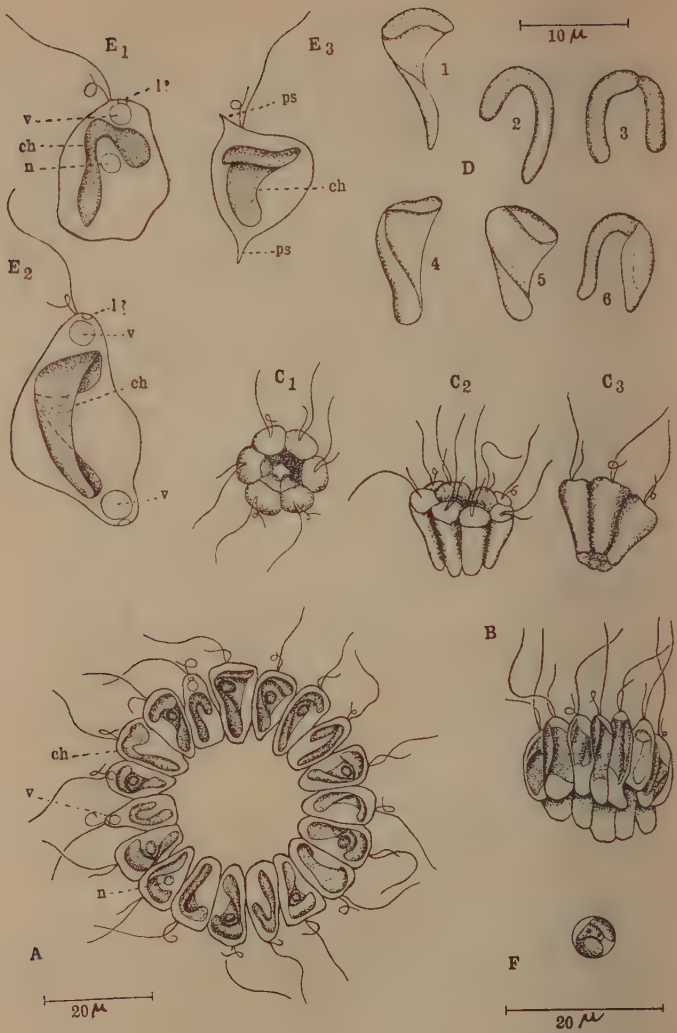
Cyclonexis annularis Stokes, until now the sole representative of its genus, is an uncommon and not well known alga. An alga, which was at first regarded as this species, was found in spring in a Hertfordshire pond in two successive years (Jane, 1937) and afforded limited opportunities for study, although its life-history could not be investigated completely owing to failure to keep the organism alive for more than a day or so.

In this new species, for which the name *Cyclonexis erinus* is proposed, the cells are attached laterally to one another, forming an annular or ellipsoidal colony composed of from six to twenty-five or even thirty cells (figs. 1, A–C; fig. 2); colonies of 10–20 cells were most frequently observed. When the colony consists of few cells it has a compact appearance, the cells being united along the whole of their lateral surfaces; these smaller colonies are somewhat conical in shape, with the flagella situated at the broader end (fig. 1, C_{1-3}); in the larger colonies, however, the cells tend to be less compactly united (fig. 1, A; fig. 2), while they lie with their long axes more at right angles to the plane of the colony, although at times even the larger colonies have a slightly conical form. Sometimes the larger colonies do not lie wholly in one plane, and such colonies, seen from the side, appear to sag, either at the edges or in the middle.

The most characteristic mode of progression is a forward movement, with the flagella foremost, this movement being accompanied by a fairly rapid rotation of the colony; at times the rotational movement alone seems to be sufficient to propel the colony, somewhat erratically, through the water.

In comparing *C. erinus* with *C. annularis*, Stokes's figures of the latter, which appear to be the only ones available, together with his original description (Stokes, 1886), must serve as a basis for comparison. *C. erinus* has larger cells and the colony a greater diameter. In *C. annularis* the cells are, to judge from the figure, arranged in the colony in a very regular manner, much more so than in *C. erinus*, but it may perhaps be questioned if there is any real difference in this respect: if the delineating of *C. annularis* proved as difficult as that of *C. erinus*, Stokes's figure may well be somewhat diagrammatic; thus my fig. 1, A, although outlined with a camera lucida, does not portray the colony in as life-like a manner as figs. 1, C_{1-3}, and figs. 2, which are redrawn from sketches of living colonies.

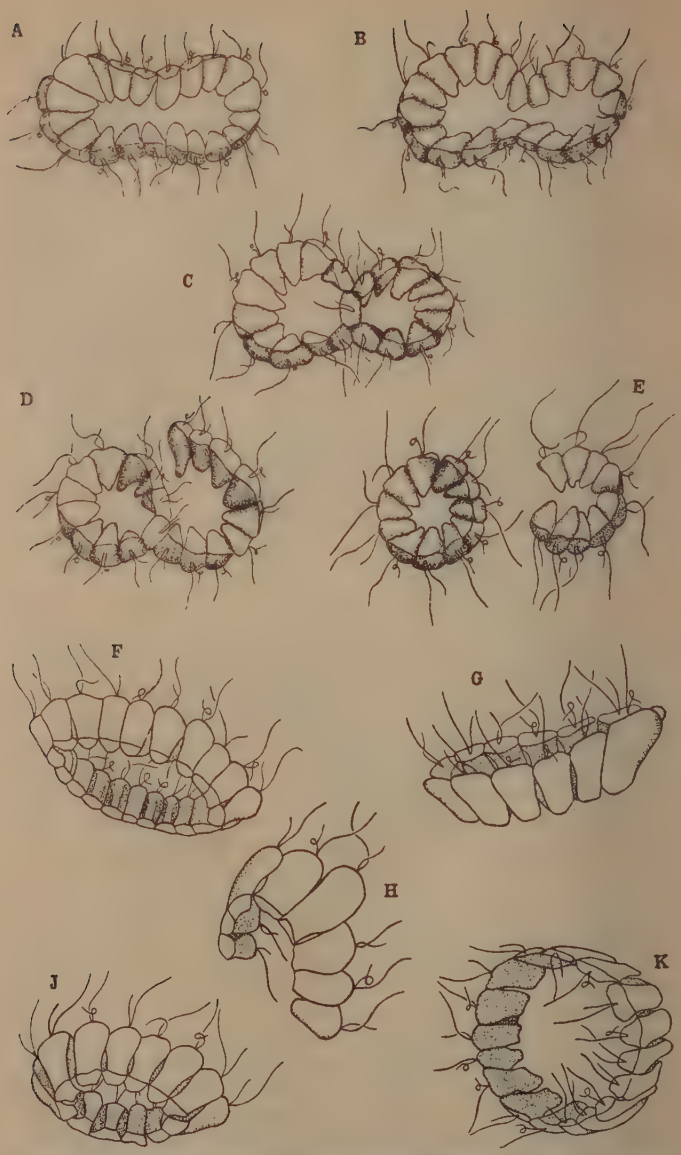
Each cell possesses two flagella, of which one is long and fairly straight and the other shorter and often curled. The longer flagellum does not move rapidly, but undulates gently, while the shorter one lashes violently. The movement of the longer flagellum so closely resembles that of certain uniflagellate Euglenoids, in which the undulatory movement of the flagellum produces a forward movement, that it seems reasonable to assume that the long flagella are responsible for the forward movement of the colony, while the shorter ones are concerned with rotation, a conclusion in keeping with Petersen's view (Petersen, 1918 and 1929). Unlike those of *C. annularis*, the flagella do not arise from a small conical anterior protuberance.



FIGS. 1, A–F.—*Cyclonexis erinus*. (A) Camera lucida drawing of a colony, the scale adjacent; the colony is somewhat flattened. (B) Camera lucida drawing from the side. (C_{1-3}) Freehand drawings of small colonies, C_1 from above, C_2 and C_3 from the side. (D 1–6) Chromatophores showing characteristic shapes produced by rolling of edges, the scale adjacent. (E_{1-3}) Cells from a moribund colony. (F) Possible cyst, the scale adjacent. *ch.* chromatophore; *l.* leucosin; *n.* nucleus; *ps.* pseudopodium; *v.* vacuole.

As the organism must be examined alive, and the colonies are in constant motion, it is not easy to study the cell structure, and this difficulty is increased by the extreme transparency of the cells. The nucleus is rather small, and is situated either in the middle of the cell or somewhat more anteriorly. There is no eye-spot ; but a small refractive granule, presumably a leucosin grain, could sometimes be made out, situated near the base of the flagella. In active colonies vacuoles were not observed in the cells, although these appeared when a colony began to break up (see below). It is in its chromatophores that *C. erinus* differs most strikingly from *C. annularis* : in the latter species each cell has two lateral laminate chromatophores, while in *C. erinus* there is only one, in the form of a golden brown plate (figs. 1, A and D). The plate is rarely flat ; one or both lateral edges may be rolled over (fig. 1, D 4), or the anterior or posterior edge may curl similarly (fig. 1, D 5). Sometimes all four edges are rolled, while at the same time the chromatophore is bent on itself, so that it has the appearance of a rolled U-shaped structure (figs. 1, D 3 and D 6) ; in such a condition the chromatophore might possibly be mistaken for two lateral ones, but only if examination were superficial.

Division of the colonies takes place while they are in motion and is a fairly rapid process, being completed in about thirty minutes (figs. 2, A–E). Large colonies, of twenty cells or more, are frequently oval in shape, and this change from the circular outline is probably a prelude to division. Division consists of the gradual approximation of opposite sides of the colony until it assumes an 8-shaped form, when the two halves, after some minutes, separate as two ring-shaped colonies, consisting of about the same number of cells. Thus a twenty-four-celled colony broke into halves consisting of eleven and thirteen cells respectively, and one of twenty cells into a ring of nine and another of eleven cells. Large colonies are frequently broken at one point, but division takes place in much the same manner, one of the free ends joining to a cell approximately in the middle of the broken colony, and the circular colony thus formed separating from the rest of the cells which soon join up to form a complete ring. It has already been noted that small colonies may consist of as few as six cells, although the cells are as large as those of the larger colonies ; these may arise from division of small rings, consisting of a dozen or so cells, in the manner just described, or from a large colony in which the apportionment of the cells has been more unequal than usual. They may, of course, actually be young colonies, formed from encysted stages. Division of the cells is undoubtedly longitudinal.



Figs. 2.—*Cyclonexis erinus*. (A–E) Stages in division of colony. (F–K) Colonies. The drawings in this figure and those shown in C, fig. 1, were constructed from freehand sketches of living colonies made for me by Miss S. Burley.

Cyst formation has not been observed, but there is some evidence that the colony breaks up into isolated cells, each of which forms a cyst. Small, empty-looking cysts, which somewhat resemble those of *Synura* in their smooth walls and spherical shape, are not uncommon in collections containing *Cyclonexis* (fig. 1, F); such cysts contain a single chromatophore, and apart from this are seemingly structureless and remarkably transparent; on one occasion some individuals of a broken-down colony were observed to take on a similar form. These cysts, however, may have belonged to some other member of the Chrysophyceae inhabiting the same locality, and until such time as *Cyclonexis* can be grown in culture, free from other Chrysophycean forms, this doubt as to the exact nature of its cyst is likely to remain.

Cyclonexis erinus is extremely intolerant to any environmental changes. It is often sufficient to keep colonies under the microscope for an hour or so to bring about their breakdown. Of the numerous reagents and fixatives with which the organisms were treated, none was found to preserve either the colonies or the cells; chloroform water (one drop of chloroform in 10 c.cm. of water) proved the least inimical, but even this was far from satisfactory. Nevertheless, it is difficult to believe that the cells are loosely attached to one another and break apart easily, for colonies seem to be unaffected by collisions with dinoflagellates, rotifers and other relatively large organisms with which they resort, and one colony was observed which was caught in the ciliary currents of a rotifer, and repeatedly drawn against the corona and swept away again, without suffering any apparent ill-effects.

When a colony breaks up, either from having been kept on a slide too long, or after treatment with very weak chloroform water, the individual cells first round up and vacuoles appear (fig. 1, E_1); there is generally a prominent anterior vacuole and often a posterior one as well (fig. 1, E_2); these vacuoles have not been observed to contract: the cell loses its rounded outline and pseudopodium-like outgrowths then appear (fig. 1, E_3), these changes preceding complete disorganization of the cell, which sometimes has the appearance of dissolving in the surrounding water. There is no reason to think that these pseudopodium-like outgrowths are formed in healthy cells, but they do not represent post-mortem changes, for the flagella during this time are moving. If the conclusion of Chambers (1924), that protoplasm is miscible with water, be accepted, it may be suggested that such changes, preceding as they do the apparent dissolution of the protoplasm in the surrounding water, are associated with the breakdown of the plasmatic membrane, which in *C. erinus* is in some way different from that of the usual naked cell.

C. erinus was found in May 1936, and again between April and June 1937, in a *Sphagnum* swamp at Brickett Wood, Hertfordshire; the swamp dries out in normal summers. Measurements of the hydrogen ion concentration were made in May and June 1937, and remained constant at 4·3 in spite of rapid evaporation at first and then fairly extensive flooding. The intolerance of the organism to treatment of all sorts suggests that *C. erinus* is adjusted to a set of very special conditions, and that its apparent rarity is due to the infrequent occurrence of these conditions. The high degree of acidity of the water at Brickett Wood might, it was thought, be one of the factors conditioning the appearance of this organism; but this is not so, for Professor T. M. Harris subsequently informed me that he had found an organism which agrees with my description of *C. erinus* in the Reading district in spring: this was found in a temporary pond where the hydrogen ion concentration was about 7·0 and the water fouled by cattle.

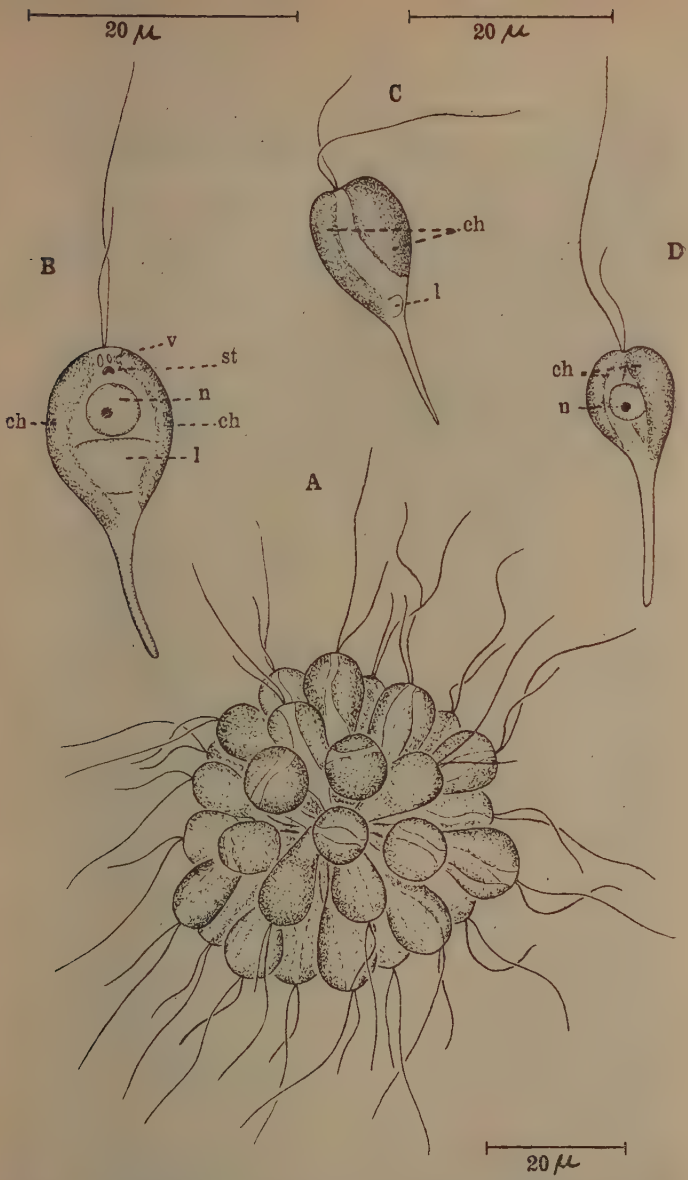
The inclusion of this new species in the genus *Cyclonexis* necessitates a revision of the generic characters. An amended description of the genus, following as closely as possible that of the original, is given below, together with a description of the new species.

CYCLONEXIS Stokes, emend. Jane. *Cellulae* a latere inter se adherentes colonias aut annulosas aut ellipticas, per se natantes, facient. *Flagella* duo imparia; quod longius, molliter undosum est, quod brevius, interdum in spiram factum, violenter flagellat. *Chromatophora* unum aut duo. Stigma abest.

C. erinus, sp. nov. *Colonia cellularum* 6–30; coloniae minores sensim infundibuliformes, spatio medio parvo, majores cellulis minus compactis et spatio medio pro magnitudine majore. *Cellulae* cuneatae vel obovatae, paene bis longiores quam latae, parte anteriore plerumque majore quam posteriore et aliquanto rotundata. *Flagellum* longius est aeque largum ac—vel paulo longius quam—cellula; flagellum minus est dimidio minus et interdum tortum ut cauda suis; chromatophorum est lamina una, saepe ad margines recurvatum, et interdum penitus involutum.—Cellulae 13–16 μ longae, 6–8 μ latae. Coloniae diametro circiter 50 μ. Cellulae per longitudinem divisae. Colonia in duas partes fere aequas constrictione divisa est.

Synochromonas elaeochrus.

The colonies of this alga (fig. 3, A), are usually markedly spherical, and move relatively rapidly with a rolling motion. They consist generally of some 50 cells, although smaller



FIGS. 3.—*Synochromonas elaeochrus*. (A) Colony. (B–D) Single cells from the colony ; C and D were fixed in Noland's fluid. *ch.* chromatophore ; *l.* leucosin ; *n.* nucleus ; *st.* eyespot ; *v.* vacuole. A scale is adjacent to each figure.

colonies of from 20 to 30 cells are often seen : one colony observed was flattened along one axis, and thus had the appearance of a thick disc ; there was no reason to regard this as an unhealthy colony.

The cells are more or less pyriform (figs. 3, B–D), but taper into a long stalk toward the centre of the colony. The periplast is smooth. There are two lateral, olive-brown chromatophores, which together almost encircle the cell, but which do not extend into the stalk region. Of the two flagella the longer rather exceeds the length of the cell, the shorter is somewhat more than half as long as its fellow. These flagella are extremely difficult to see in the living specimens ; in fact, it was only with the use of Noland's fluid that they could be satisfactorily studied. The nucleus, in which a nucleolus can often be seen, lies somewhat anteriorly, and is considerably larger, relative to the size of the cell, than that of any other member of the Chrysophyceae with which the author is familiar. There are two minute tear-shaped vacuoles in the anterior part of the cell, and normally there is no eye-spot ; the cells of one colony, however, showed a small anterior eye-spot, and occasionally there were present in a similar position a number of minute red granules, usually in a single group. Such granules may, perhaps, be regarded as an incipient or diffuse stigma, which may occasionally develop as a discrete cell-organ in this species. It may be recorded that on one occasion the author observed similar red granules in colonies of *Synura* ; these, similarly, occupied an anterior position, and are probably likewise to be regarded as a diffuse or incipient stigma. The leucosin takes the form of a large rhomboidal granule immediately posterior to the nucleus ; occasionally two such granules, lying one above the other, may be seen.

When the colonies reach large dimensions, they become ovoid in form and separate across the middle into two parts, much as in *Synura*.

Cysts have not been found, although on several occasions I have carefully searched the mud for anything which might be regarded as cysts of this species. Korshikov's observations on *S. pallida* (Korshikov, 1929) indicate that the colonies break up into individual cells before cyst-formation takes place, and if the same occur in *S. elaeochrus* the cysts might easily be overlooked.

S. elaeochrus was found in summer in stagnant water at Mimm's Wash, Middlesex ; the water, which is used extensively by farm stock, was a portion of a partially dry stream, and the abundance of euglenoid flagellates suggested that it is rich in organic matter. *S. elaeochrus* was very localized in its occurrence, and was found among the water plants, chiefly

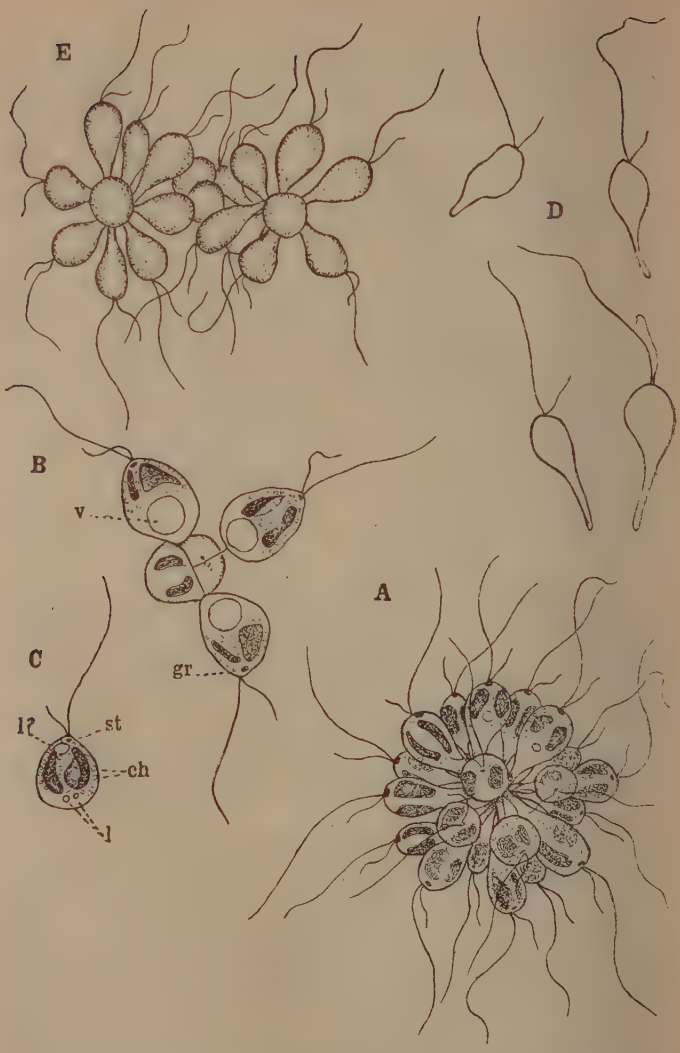
among *Elodea canadensis*; it was present in abundance in one dip made on August 23rd, 1938, but on succeeding visits very few colonies were found, and none at all after September 2nd.

S. elaeochrus differs in many minor points from *S. pallida* Korsh. (1929), the only other species of the genus. These differences may best be brought out by comparing the two species in tabular form :—

S. pallida.	*S. elaeochrus.*
Colonies embedded in mucilage.	Colonies without mucilage.
Colonies composed of about 40 cells.	Colonies composed of about 50 cells.
Cells asymmetrical and with obliquely truncated anterior end.	Cells symmetrical and with rounded anterior end.
Long flagellum five times as long as short one.	Long flagellum scarcely twice as long as short one.
Chromatophores small, laminate, waisted.	Chromatophores large, laminate, not waisted.
Stigma usually present.	Stigma usually absent.
Nucleus small.	Nucleus large.
One anterior contractile vacuole.	Two anterior vacuoles.
Nutrition both holophytic and holozoic.	No evidence of holozoic nutrition.

Synochromonas elaeochrus, sp. nov. *Cellulae* piriformes, stipite posteriore, circiter 24 μ longae et qua parte latissimae circiter 9·5 μ latae, junctae in colonias globosas, diametro circiter 50 μ, cellularum 20–50, muco non circumdatarum. *Flagellum* majus paulo longius quam cellula ; flagellum brevius est aliquanto majus quam dimidia pars. *Periplastus* est teres. *Chromatophora* duo, lateralia et laminata. *Nucleus* magnus et in loco anteriore. *Vacuoli* duo, minuti et anteriores. *Stigma* plerumque abest. *Leucosin* plerumque formam granuli rhomboedalis post nucleum positi habet. *Cysti* ignoti. In stagno habitat.

In May 1936 Professor T. M. Harris sent me a colonial flagellate which he had found at Reading. The organism was obviously a *Synochromonas* and resembled Korshikov's *S. pallida* more closely than the species just described. The cells were similar in shape to *S. elaeochrus*, although tending to be truncated anteriorly in some individuals (figs. 4, A and D), and the short flagellum was about a third as long as the long one. In their dimensions the two olive-brown laterally placed chromatophores approached those of *S. pallida*, from which, however, they differed in that they were not narrowed medially. In some colonies an anterior stigma was present. The leucosin granules varied in their position ; sometimes small rounded ones were situated posteriorly, at other times smaller ones occupied an anterior position. As in *S. pallida*, the outer protoplasm of this Reading form was granular, but the colonies resembled *S. elaeochrus* in their freedom from mucilage. The



FIGS 4.—*Synochromonas* cf. *pallida* Korsh. (A) Typical colony. (B) Four-celled colony with very tenuous connections between cells; possibly moribund. (C) An isolated cell. (D) Outline drawings of four cells from a colony, showing characteristic shape. (N.B. The shape of C is not characteristic.) (E) A colony dividing into three parts of 6, 8 and 9 cells respectively. *ch.* chromatophore; *gr.* granule; *l.* leucosin; *st.* stigma.

colonies were about 70 μ in diameter and the individual cells about 21 μ long and about 9 μ broad in the widest part of the cell.

Division of the colonies took place in the usual manner, with about half the cells passing to each daughter colony, but in one instance a colony was observed to divide into three parts containing six, eight and nine cells respectively (fig. 4, E). In one colony, which consisted of only four cells, the cells were rounded posteriorly except for an extremely tenuous 'tail' region (fig. 4, B); the cells of this colony showed a large vacuole situated posteriorly, and I am inclined to regard this as a colony in the early stages of disintegration; this is suggested by the tenuous stalks and the presence of the large vacuoles (cf. *Cyclonexis*, p. 304).

It seems probable that this organism represents a third species of the genus, but until it is possible to study it in further detail it seems undesirable to give it specific rank; it is, therefore, referred for the present to *S. pallida* Korsh.

Literature cited.

Chambers, R. 1924. The Physical Structure of Protoplasm as determined by Micro-dissection and Injection. In Cowdry, E. V., 'General Cytology', Chicago.

Jane, F. W. 1937. Some Hertfordshire Flagellates, I. *Trans. Herts. Nat. Hist. Soc.* xx, pp. 133–40.

Korshikov, A. A. 1929. Studies on the Chrysomonads, I. *Arch. Protistenk.* lxvii, pp. 253–90.

Petersen, J. B. 1918. Om *Synura Uvella* Stein og nogle andre Chrysomonadiner. *Vidensk. Medd. Dansk. Nat. Foren.* lxix, pp. 345–57.

—— 1929. Beiträge zur Kenntnis der Flagellatengeisseln. *Bot. Tidsskr.* xl, pp. 373–89.

Stokes, A. C. 1886. Notices of New Freshwater Infusoria. *Proc. Amer. Phil. Soc.* xxiii, pp. 562–8.

ON THE BIOLOGY OF TWO LATRODECTUS SPIDERS IN PALESTINE.

By A. Shulov, Department of Zoology, Hebrew University, Palestine.

Latrodectus tredecim-guttatus (Malmignatte).

External features.—Female. The abdomen is globose and the legs are long and strong. In Palestine the body and legs of this variable spider are coal black in colour and covered with small velvety hairs. The younger instars are ornamented with 13 red spots arranged in three longitudinal rows on the back of the abdomen. The maximum length of the female is 12 mm. (and including legs 51 mm.).

In contrast to the female, the red spots are generally conspicuous on the adult male's abdomen. The body can attain a length of 4 mm.

Distribution.—In Palestine this species is to be found in strong dusty webs under large stones, as well as in the holes of rodents, near the roots of shrubs, and, rarely, in the corners of old buildings and in the entrance of caves. The webs are never found among shrubs, as is the case in other countries. The female spider sits in the deepest part of her web together with her white cocoons. There she builds a 'retreat', a short tube open at both ends. But often this 'retreat' is closed at one side and is bell-shaped.

In this country it has been found on the hills, in the coastal plain, in the Plain of Esdraelon, in the Judean desert, and in Transjordan.

Egg-sac.—The female encloses her eggs in a white globose sac 14–17 mm. long and 12–15 mm. wide, pointed on one side. On the outside it is covered with a smooth envelope, fine but tough, with the strength of parchment paper. Inside this envelope there are strong, golden, cotton-like threads, enclosing a small 'dish' of eggs. The eggs which do not develop, possibly because they are unfertilized, may be easily recognized by their peculiar orange colour.

Thirteen egg-sacs were examined, and it was found (*a*) that the number of eggs in a sac varied from 84 to 452 ; (*b*) that the average number of eggs was 235 ; and (*c*) that 15 per cent. of the eggs did not hatch.

The results of the examination of a number of cocoons.

Cocoon No.	1	2	3	4	5	6	7	8	9	10	11	12	13
No. of eggs	323	305	452	250	289	276	247	202	84	126	246	152	109
No. of developed eggs.	319	173	256	212	289	276	247	200	84	89	243	116	105

Average number of eggs per cocoon (mean of 13 cocoons) : 235.
Percentage of hatched eggs : 85.

According to this table the number of eggs varies between 84 and 452.

Each female can lay seven to eight times and probably more. The interval between one egg-laying and another depends on the quality of food consumed by the female, but she does not lay eggs more often than once a week.

Development.—The eggs hatch in from 17 to 39 days. The calculation of these results gives a hyperbolic curve with a threshold of development of 17° C. and 113 days-degrees of effective temperature (after Blunck-Bodenheimer).

The body of a hatching spider is pale violet, and the legs are white. They move very slowly, and scarcely change their position in the cocoon. In June and July this stage lasts five to six days.

The spider of the first instar moults without difficulty. In no case investigated at this stage were any dead spiders found in the cocoons. After moulting they at first keep their original colour, but within 10 to 12 days turn black, with bright reddish spots. They sometimes remain in the cocoon for 14 days in summer and two to four months in winter and beginning of spring. When favourable conditions for their development exist out of doors the spiders bore a hole in the envelope of the cocoon and crawl out. It is of interest to note that they even bore such a hole when a cocoon is torn, and it would be possible for them to get out freely. They crawl out one by one through the hole and remain for some days near the cocoon. Only feeble individuals remain inside, and, therefore, dead spiders of this instar can be found there. Sometimes single spiders crawl back into the cocoon for some days.

This instar is the most important for the distribution of this spider. After staying for some days near the cocoon they disperse in all directions and endeavour to climb upwards. The experiment of Fred d'Amour *et al.* on the dispersal of *L. mactans* by means of the wind was repeated. Thirty spiders of the second instar which had left their cocoon some days ago were put into a cylindrical glass, 1·5 metres long. When a long stick was carefully introduced into the tube the spiders immediately began to crawl upwards along it; reaching the top, some lifted their abdomens and threw a silken thread into the air, making use of the moderate wind blowing at the time. The majority, however, behaved in a manner quite different from that observed by Fred d'Amour. They allowed themselves to be blown away by the wind only after being bound for a short time to the stick by a thread. This crawling-out process can continue for up to a week, and the dispersal of the spiders for even longer. If after a relatively short time they do not succeed in obtaining food, they die, as is shown in the following series of experiments.

Of 18 spiders of the second instar the following died on being put into separate glasses :—

	In days.	
Temperature.	Average (mean of two series).	Last one.
10° C. ...	44·5±5 (92·2) *	110 (102) *
15° C. ...	25 ±3 (31·5)	39 (59)
20° C. ...	13·5±0·1 (23)	25 (30)
25° C. ...	10·8±0·1 (19·8)	18·5 (25)
30° C. ...	8·9±1 (14)	10·5 (23)

* The numbers in brackets indicate the third series of experiments with 18 spiders taken from the cocoon five days before they would ordinarily have crawled out as determined by the control.

In spite of the capacity to remain without food inside the cocoon for several months at a temperature of 15–20° C., they die relatively quickly after having left the cocoon.

The spiders reach their third instar after they have settled in a definite place. Sometimes they get through the moult without feeding at all. In the successive moults the red spots disappear in a definite order.

The female spider moults eight times and the male only five to six times. After the final moult (and sometimes earlier), the female becomes totally black, the spots sometimes leaving white rings. The male undergoes the same changes, but his spots remain more distinct. Immediately after the last moult he resembles the pre-adult female: his abdomen is quite globose, but some days later it begins to get thin till it reaches its normal shape, the juices of the body being used for the production of sperma. He succeeds only rarely in catching prey.

It sometimes happens that in the male of the fourth and fifth instars prominent palpal organs develop. In this case the body shrinks and the spider dies within a short time, without being able either to moult, to copulate with the female or to catch prey.

Examples of development.

	Day of oviposition.	Day of leaving the cocoon.	Period in the cocoon (days).	Day of maturity.	Development outside of the cocoon (days).	The total period of development (days).
Brood 3:						
♀ min.	15. xii. 33	8. iv. 34	115	15. vii. 34	99	219
Brood 3:						
♀ max.	,,	,,	115	16. x. 34	190	305
♀ average ..	,,	,,	115	27. viii. 34	140	255
♂ average ..	,,	,,	115	12. vii. 34	96	211
Brood 4:						
♀ average ..	8. vi. 36	19. vii. 36	41	22. x. 36	93	134
Brood 5:						
♀ average ..	1. x. 36	20. i. 37	112	1. x. 37	253	375*
♂ average ..	,,	,,	112	11. viii. 37	203	315*
Brood 6:						
♀ average ..	5. x. 36	16. iv. 37	193	30. viii. 37	136	329
♂ average ..	,,	,,	193	,,	136	317

* Ganigar (Plain of Esdraelon).

The development of these spiders is not strictly related to a definite season of the year. The female with the cocoon is to be found throughout the whole year, but mostly in the winter. As already stated, in the hills the young spiders remain in the cocoons, in winter and early spring, for some months after having changed their colour. In the Plain of Esdraelon they may leave the cocoons as early as January. Thus the development of the spiders from the egg to maturity takes

at least 255 days from eggs laid in the winter, and only 134 days from eggs laid in the spirng.

The conclusion based upon the above table is that in optimal conditions *L. tredecim-guttatus* produces two generations a year, and under normal conditions one and a half, or one generation. The offspring of the female which had laid her eggs in the winter reached maturity in eight months, while the succeeding generation became adult under the most favourable conditions before the next winter.

In the Eremian zoogeographical region of Palestine (22·1° C. in average) the possibility of development approaches two generations. In the Mediterranean zone (16·9° C. in average) the development of one generation lasts one year, though under optimal conditions there may be two generations per annum.

The female of *Latrodectus tredecim-guttatus* can live for one year and a half and even more. The male lives only 40 to 50 days. After this period he dies, whether he has copulated or not.

The use of the cocoon.—Observations as to why the young spiders remain in the cocoon raise two questions :—

A. Does the cocoon protect the eggs and young spiders against unfavourable influences of environment, such as excessive warmth, humidity, enemies, and parasites ?

B. What stimulates the spider to leave the cocoon ?

The following experiments were made :—

(1) Four experiments were made with eggs left in the torn cocoon under conditions of 30 to 40 per cent. R.H. At temperatures of 15° C., 20° C., 25° C., 30° C., and 35° C. no eggs developed.

(2) Three cocoons with eggs were put immediately after oviposition in a temperature of 23° to 26° C. and 60 per cent. R.H. Two of them were opened with scissors and were left open, and the third was opened 15 days after oviposition only and enclosed again. The latter was again opened only for observation. The results coincided, as the following table shows :—

Comparison of development of eggs in the opened cocoons and in the closed ones.

Day of oviposition.	Day of hatching.	Development of eggs (in days).	First moult.	Duration of the first moult instar.	Left the cocoon.	How many days after the moult.	Remarks.	Temp.
8. vi. 36	29. vi. 36	21	5. vii. 36	6	19. vii. 36	14	Open	24° C.
7. vi. 36	4. vii. 36	17	9. vii. 36	5	22. vii. 36	13	Open	25° C.
5. vi. 36	12. vii. 36	17	17. vii. 36	5	30. vii. 36	13	Closed	26° C.
4. ix. 37	2. xi. 37	39						20° C.

(3) Four cocoons, containing normally coloured spiders, were divided among the thermostats of 30° C., 25° C., 20° C., and 15° C. Each cocoon was put into a glass upon wet sand, which was allowed to dry. The glasses were then closed tightly and low humidity prevailed in them. After five months all the spiders were found dead inside the cocoon.

(4) Two cocoons with spiders of the second instar immediately after the moult were put in a temperature of 32·6° C. and 20·4° C., at 80 per cent. R.H. The spiderlings left the first after ten days and the second after 25 days.

(5) Of the various broods, it may be stated that the spiders hatching in the winter remain in the cocoon for four months, and those hatching in the summer for 35 to 41 days only.

(6) From numerous broods the following ecological data have been worked out for the hyperbolic curve after Blunck-Bodenheimer.

	c (threshold).	Th.C. (effective temp.) (days-degrees)
Development of the eggs....	17	113
The first instar	10	90
From the first moult till leaving of the cocoon	14 (12·3)	168 (203)
Post-cocoon development....	16·7	565·8
	16·2 (calculated at 20° C.)	
	16·4 (calculated at 25° C.)	
	16·1 (calculated at 30° C.)	
	Total	936·8

$t(T-c) = Th.C.$: t = time ; T = temperature ; c = threshold of development ; Th.C. = effective temperature.

(7) Numerous observations of the cocoons show only two cases of parasitism, by an ichneumon determined by Ch. Ferrière (British Museum) as '*Eurytoma* sp., probably new or genus nov. (near *Bruchophagus arachnophaga* Gir. from Australia)', but in the torn cocoons mould develops which destroys the eggs.

These experiments, together with the observations made under natural conditions, allow the following conclusions to be drawn :—

(*a*) The envelopes of the cocoon allow the warmth to penetrate, but at the same time conserve the humidity necessary to the eggs and the young spiders.

(*b*) The envelopes may mostly protect the spiders from parasites and enemies. As those of the first instar and the beginning of the second move slowly, they would be easily destroyed without this means of protection.

(*c*) The effective temperature needed for leaving the cocoon is 168 (203) days-degrees under the corresponding conditions of humidity.

(*d*) The fact that some of the spiders remained in the cocoons for a long time before leaving them may be looked upon as a false diapause or an interruption of development during unfavourable external conditions.

Sexual life.—Copulations of this *Latrodectus* were observed on 4, 10, and 31 July 1934, 18 August 1937, 4 September 1937. The observations were continued from 3 to 14 hours each. They all confirm those made by Prof. U. Gerhardt. The male calms and hypnotizes the female by shaking the web with his legs. He then swaddles her with fine threads. The female at first either responds with slow movements of her legs, or brushes off the threads and leaves the place of copulation. When the female ceases to move, and is 'swaddled' enough, the male 'drums' upon her body until she turns on her back. The male then approaches the genital opening of the female, 'drums' near it and lifts his body, protruding his pedipalps downwards and backwards. He then begins to attack the female with his pedipalps, introducing one finally into the genital opening of the female. The insertions of each pedipalp alternately continue mostly for 20 to 30 seconds, but are sometimes prolonged to 37 minutes.

The process of copulation usually ceases after two to three hours, but sometimes continues for as long as seven hours. On occasions when the male does not succeed in withdrawing his palp in the time he is devoured by the female.

In general the female awakes some minutes after the male has finished his attempts. If after one male has finished the process, another is put into the glass, copulation takes place again.

The absorption of sperms by the palps was not observed clearly.

Oviposition takes place at night and in the early morning.

The period between copulation and the first oviposition is three weeks, according to our experiments, but more than a year in the case of *L. mactans*, according to Fred d'Amour.

Some physiological data.—The following physiological constants were found by appropriate experiments with young spiders of the second instar: Instantaneous thermal death, 47·1° C.; cold torpor (freezing point), 1·3° C.; preference temperature, 29·8° C.

In order to determine the reaction of the spiders to the light, 16 spiders were put for an hour into a glass tube 20 cm. long and 5 cm. wide. Half of the tube was covered with a black

cloth. The position of the spiders was recorded every ten minutes. The results were as follows :—

(1) Spiders which left the cocoon a day previously (in 12 experiments among 13) when put in diffused light of the room show a graduated but clear accumulation in the bright part.

(2) Spiders, as before, put under direct rays of the sun (two experiments) passed almost immediately to the bright half.

(3) Spiders taken out of the cocoon and put in diffused light of the room accumulated in the bright part (three experiments).

Conclusion.—A clear helio- and photo-taxis is shown by young spiders of the second instar which have left the cocoon or are about to leave it.

Food.—The following examples are included to show which remnants of prey may be found in the webs of the adult *Latrodectus* in its natural habitat :

(1) *Monomorium* sp. (Formicidae), *Musca domestica* 2, *Pimelia mittrei* 4.

(2) *Pimelia bajula* (Coleoptera), *Forficula lurida*, *Porcellio* sp., *Hemilepistus* sp. (Isopoda), *Textrix* (Araneidae, Agelen).

(3) *Opatrum libani*, *Coniocleonus excoriatus*, *Calathus fuscipes* (Coleoptera).

(4) *Pimelia bajula*, *Tentyria* ssp., *Dendaurus* sp., *Onthophagus* ssp., *Pachyscelis rotundata*, *Carabus impressus* (Coleoptera), Acrididae larvae, *Heterogamodes* (Blattidae), *Sehirus dubius* (Heteroptera), *Messor semirufus* 5 (Formicidae), 5 diverse spiders, *Scorpio* 2·5 mm. in length, *Buthus* 7 mm.

The adult female catches her prey in the web, but the adult male eats hardly at all, and if it sometimes does it does so outside the web only.

The female ceases to eat two days before oviposition.

The amount of venom.—The great interest aroused by this spider both among laymen and among scientists is due to the unusual severity of its venom. According to observations of Russian naturalists, such as Rossicow, Motschulsky, Schtschesnowich and others, the bite of the Black Widow causes considerable losses to herds of cattle, horses, and camels, which are killed in the pastures.

The bite of this spider may in serious cases be fatal to human beings. In less serious cases the acute pains and disturbances of metabolism weaken the body for two to three weeks. The general weakness remains for one to two months. The acute pain radiates from the place of the bite, and after two hours invades the whole body, giving rise to the following

symptoms : breast cramps, cold perspiration of the forehead, and cyanosed skin. Acute attacks of pains in the bones follow each other every five minutes. After some hours the pains diminish, and in two to three days disappear altogether.

There are contradictory opinions, particularly among western scientists, concerning the amount of venom. Their experimental animals did not suffer or suffered very little from the bites of the Black Widow. One experimenter felt no pain when bitten. In the opinion of Rossicow, there is a great difference between the amount of venom in the Asiatic spider and the European one. A certain theory which supports this last opinion maintains that these differences depend on the conditions of environment, and are, therefore, subject to periodic changes.

Veillard, after reviewing all the literature, came to the conclusion that a big amount of venom exists in the glands of this spider. Recently I was informed by Dr. Kleinschmidt that a grave case of bite by *L. tredecim-guttatus* was cured by him in Padua (Italy).

The following questions were investigated in the case of the Palestinian species :—

A. What is the amount of venom in the glands ?

B. Does breeding in the laboratory affect the amount of venom in this spider ?

C. Does the state of nutrition (of repletion or otherwise) affect the venom ?

In our experiments 26 adult female spiders and 80 laboratory animals were used. The spiders were held in broad pincers in such a way that they could insert their jaws into the shaved skin of animals. Two bites were allowed in order to diminish the possible variation during each. The place of the bite was always the right side of the belly, 1–2 cm. from the hind right femur. Each bite lasted for two to three seconds ; in each case it was necessary to push the spider backwards in order to pull out his jaws from the skin of the bitten animal. From the following table it is clear that :

A. The venom of the Palestinian spider is dangerous even for five field-mice bitten in succession by the same spider. It is dangerous, but not always so, for guinea-pigs, white mice, and rats. This amount of venom may be renewed in three days and even earlier. The experiments with white mice showed a clear diminution of the strength of the venom.

B. The general impression is that there is no significant difference between the spiders bred in the laboratory and those caught in the field.

C. The state of nutrition of the spider does not influence the strength of venom if it is in a good condition in general.

The effect of the venom of the *L. tredecim-guttatus* as has been described by various authors was confirmed by our experiments, namely, swift paralysis of the legs, heavy respiration, strong salivation, and violent contractions of the diaphragm, with heavy perspiration of the head and bristling of the hair. The bitten animal lies down, and in fatal cases succumbs mainly from asphyxia following paralysis of the nervous system. If it recovers, it is gradually, after one hour.

Summary of experiments made with venom. Strength.—Number of animals killed when bitten successively by the same spider: white mice, 2 (2), 2 (4); field mice (*Microtus guenteri*), 4 (4), 3 (3), 4 (4), 5 (5), 2 (4).

The figures in brackets indicate the number of animals bitten.

Bitten by separate spiders:
rabbit, 0 (2); rats, 1 (3), 0 (1), 0 (1); *Mus musculus*, 1 (1); guinea-pig, 3 (6).

Comparison between spiders bred in the laboratory and those found in the field.—In laboratory: white mice, 7 (9); field mice, 5 (6); found in the field, 5 (8), 3 (3).

Comparison between spiders in varying states of nutrition.—Well fed: White mice, 4 (5); undernourished (but in good health), 4 (6).

The strength of venom in the male and in the young spiders could not be investigated because I did not succeed in getting them to bite.

An experiment was made to calculate the amount of venom by a chemo-pharmacological method. The content of the venom glands was macerated in a physiological solution and then injected into field mice and rats. The results areas follows:—

Field-mice M.L.D. per 1 gr., 0·006.—The content of the glands of one spider is 167 M.L.D. per gm. of mouse.

White rats. M.L.D. per 1 gr., 0·004.—The content of the glands of one spider is 250 M.L.D. per gm. of white rat.

In Palestine this spider is known but little, although it is well distributed in the hill region. It is possible that cases of illness caused by this spider have occurred without their real cause being known. One case of serious illness of a man bitten by *L. tredecim-guttatus* has been described.

LATRODECTUS PALLIDUS Camb.

Moderate-sized spiders with a large smooth abdomen. Cephalothorax brownish-yellow, darker at the sides. The abdomen is a beautiful white on its dorsal surface. Six traces of the muscular insertion are seen as black-brown points.

The sides of the abdomen are brownish-yellow. The ventral side is whitish-yellow with black points in the middle. The epigyne is big and its opening oval transverse in form. The legs are yellowish, with brown rings at the joints. The tarsi are brown. The length of the body is from 7 to 10 mm.

In the male the yellow colouring of the sides of the body and of the rings of the legs is fainter. He very much resembles the young females of the same species. A full description of this spider has been given by O. P. Cambridge who was the first to describe it.

Distribution.—It was originally described from Palestine by O. P. Cambridge (Jordan Valley, 1872), and found again by Festa in Jericho (1895). I found it in greatest numbers in the neighbourhood of Ganigar (Plain of Esdraelon) in the years 1934 to 1937, and near Tel Aviv. I am grateful to Prof. E. Reimoser for information on its distribution in other countries, such as Tripolitania, Persian Gulf, Egypt, and Syria.

Previous biological data.—As far as I know, nothing has yet been published about the biology of this spider.

Web.—Contrary to the statement of O. P. Cambridge that adult and immature females were found ' in irregular snares spun among low plants on the plains of the Jordan ', it is possible to state that in all cases of observation highly complicated webs were found. This fact is especially interesting because in other species of *Latrodectus* and in all other Theridiidae the spiders webs are irregular or only traces of regularity are found.

The web of *L. pallidus* consists of three parts: the ' retreat ', the ' retort ', and the ' corridor '. The thimble-shaped ' retreat ' is spun from white, thin, and opaque material. It is 20 mm. high and at the base 25 mm. wide; and was found in all cases investigated (about 40). The retort, too, is built in the shape of a thimble, the top of which is formed by the retreat, and its base is bent into the form of a chemical retort. This lower part is spun from thick threads forming a thin, partially transparent web. On one side is a round entrance-hole. The retort is covered with viscid threads, which are renewed by the spider from time to time. The last part is the ' corridor ', spun from single threads and forming a wide tube, which tapers towards the ' retort ' and serves as a passage to it. Only a web spun by adult females is composed of the three parts described above. Young females spin only the two first sections, and the very young ones and the males restrict themselves to a single ' retreat ' surrounded by a few threads.

The old females, sitting on shrubs near the tracks of ants,

build an additional web for catching them. They spin threads in the form of a triangle between three shrubs intercepting the tracks of the ants. Through this triangle passes a wide ribbon-band, composed of a number of threads linking the middle of the base of the triangle with its apex. When ants climb up on the shrubs the spider can catch them by running along the ribbon band.

The spiders may also descend by a thread and catch the prey running in the ground. The spider sits in its 'retreat' when at rest. The prey is brought into the retort in order to suck it. The cocoons are arranged, too, inside the retort.

The web is constructed in the following way:—At first horizontal threads are spun in parallel lines. Then a number of foundation threads are erected perpendicular to the first ones. Afterwards the spider begins to crawl around spinning a 'retreat', without any help of its legs. While spinning it moves its legs periodically through its jaws. Some time after having finished the retreat it spins a retort and the 'corridor' last of all.

The egg-sacs.—The egg-sac of *L. pallidus* may be distinguished from that of *L. tredecim-guttatus* by its small diameter, reaching up to 12 mm. There are 147 eggs on the average in each, as against 235 in that of *L. tredecim-guttatus*. The number of eggs varied in the 17 sacs examined from 40 to 233 : 10 per cent. of the eggs did not hatch.

The results of the examination of a number of cocoons.

Cocoon No.:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
No. of eggs:	81	144	223	40	41	43	120	173	140	85	130	177	170	80	187	207	196
No. of larvae:	81	7	95	40	41	43	120	173	61	85	130	177	170	80	187	207	196

Average number of eggs per cocoon (mean of 29 cocoons) : 147.
Percentage of hatched eggs : 90.

The sac protects the eggs well from changes in external humidity, which may injure them.

Development.—Eggs hatch in three weeks to one month, at an average temperature of 25° C. At a temperature of 20° C. their development lasts for over forty days, and at 15° C. they begin to develop and then die. The experiments made at these temperatures show the mortality of the eggs in all humidities.

The females lay eggs throughout the year.

The relative speed of leaving of the cocoons by young spiders of L. pallidus *(in days).*

R.H.	10 %	20 %	40 %	60 %	80 %	100 %	Av.
Temperature :							
30° C.	—	10	12	8	8	8	9
25° C.	10	—	—	—	49	—	30
20° C.	—	—	52	—	111	43	65
15° C.	—	—	—	—	161	—	161
10° C.	—	—	—	—	—	195 ?	195 ?

The young spiders which hatch from the eggs are white in colour, and resemble those of *L. tredecim-guttatus* of the same instar, but are smaller than the latter. In the egg-sac they moult for the first time. In the beginning their colour resembles that of the first instar, and only after some time do the characteristic signs of the species appear.

The spiders used in these experiments were all of ' normal ' colour and were all in the egg-sac. Upon the basis of these facts a hyperbola of speed at which they leave the sac (after Blunck-Bodenheimer) was calculated: c=18·4° C.; Th.c.= 104 days-degrees.

In many cases the spiders died without having left the egg-sac. This fact has been noticed in low temperature especially. The spiders, having remained alive in the egg-sac for seven months, do not leave it even when the temperature is raised. It appears that the heat necessary for changes in their body must be applied within a certain time, and if too late the young spiders cannot leave the cocoon.

The influence of the humidity does not seem to be considerable. From the following table one can see that the high humidities accelerate the leaving of the egg-sac, but the percentage of spiders leaving is then smaller.

The influence of the humidity on the leaving of the cocoon at 30° C.

Humidity	20 %	40 %	60 %	80 %	100 %
No. of spiders which left	176	205	196	177	86
Percentage of these compared with the number of the spiders in the cocoon.	93 %	100 %	100 %	82 %	56 %
No. of days after placing in thermostat	10–12	10–12	8	8	8

The spiders do not leave the egg-sac through the cuts and torn places of the envelope. The observation made in this respect agrees with that made on *L. tredecim-guttatus*. The search for special places which the female might have left to help her offspring in boring through the wall of the sac (as in wild bees) has resulted in the conclusion that, even if there are weak places, the young spiders do not use them.

In the Plain of Esdraelon the young spiders are ready to leave in mid-February.

After having left the cocoon, the young spiders sometimes remain near it and then disperse. It seems that the manner of dispersion resembles that of *L. tredecim-guttatus*.

The speed of death of young spiders (mean), in days.

Of 20 spiders of the second instar which have just left the cocoon, the following die at

Temperature	Days (mean).	Days (last one).
10° C.	13·2	46
15° C.	19·2	33
20° C.	15·6	24·3
25° C.	12·4	16
30° C.	7·8	11·5

This table shows that the optimal temperature under these conditions is 15° C., in which the spiders can live up to 19 days without food. It is remarkable that in the lower temperatures the spiders die as in 20° C. to 25° C.

The speed of death of the young spiders in the cocoons.
(*After how many days the last spider died.*)

R.H.	10 %	20 %	40 %	60 %	80 %	100 %
Temperature :						
10° C.	—	210	263	210 ?	166	179
15° C.	—	172	304	318	259	122
20° C.	91	139	110	139	125	—
25° C.	69	59	59	59	——	—
30° C.	—	—	—	—	—	—

The sacs were investigated after each fortnight.

According to C. Hamburger the development of the digestive systems of young spiders investigated on *Argyroneta aquatica* lasts 7 to 16 days after hatching. This proceeding, without doubt, depends on temperature.

The comparison between the results obtained with the speed of mortality of the young spiders which remained in the sac and died there shows an astonishing difference. We must keep in mind that the young spiders do not devour each other inside the cocoon, and thus lack any kind of food. Those spiders which have left the sac and do not succeed in catching some prey within several days are condemned to a quick death.

Post-egg-sac development.—The young spiders leaving the sac from eggs laid in the winter remain in this instar up to May. The male moults 4 to 5 times, the female 6 to 7. In nature the females reach maturity in June and July, and if

they laid their eggs in July their offspring may reach maturity by winter. We may conclude from the above that under optimal conditions the spiders have two generations per year, though usually they have one to one and a half. The life of the male is short, even if he has not copulated. He is able to catch more prey than *L. tredecim-guttatus*.

The food and the hunt.—Upon examining the remnants of the prey sticking to the wall of the ' retreat ' and ' retort ' it may be seen that ants of the species *Messor semirufus* serve as the main food of *L. pallidus*. Also remnants of diverse beetles were found (many *Adesmia* and others), larvae of grasshoppers, Drassid spiders, *Phalangium savignyi* (Opilionid), and a scorpion, *Buthus*, 4 mm. long, were found.

The parts of the web are so arranged that the prey enters the corridor in the direction of the ' retreat ' of the spider and is there easily captured. The hunt follows the usual method of Theridiidae, and is almost similar to that of *L. tredecim-guttatus*. When the prey is caught and bitten, the spider tears the threads with which it has bound the prey to the web and carries it higher up into the retreat. Here it sucks the prey dry and then either throws it out of the web or strengthens with it the wall of the ' retort '.

An interesting case of preying upon a caterpillar of *Thaumetopoea* (a processionary moth) should be mentioned. The spider caught, swaddled, and sucked the caterpillar for some hours; thereafter the spider remained motionless. After five days the spider was found dead, his abdomen being black and swollen. A dead spider has otherwise never been observed in such a state. It appears that the spider either died from intoxication by poison juices of the caterpillar, or was seriously wounded by the poisoned bristles of the latter.

Enemies and parasites.—Mould entering the cocoon through torn places destroys the eggs. When no holes are present the mould cannot damage either eggs or young spiders. Only once were the eggs of *L. pallidus* found infested by *Eurytoma* sp. (the same species as in the case of *L. tredecim-guttatus*). *Bruchus foveolatus* was found inside a torn cocoon.

The grazing of cows and goats in an area heavily infested with *L. pallidus* near Ganigar (Plain of Esdraelon) almost freed the area from the spiders, but there are no direct observations as to whether the latter are devoured by domestic animals.

Sexual life.—Two observations on the copulation of these spiders:—

The male was placed in a receptacle with the female. He approached her, drumming upon the threads with his

pedipalps. He then passed his palps through the chelicerae and began to spin threads around the female. The female moved several times, tearing the threads, but soon assumed a position convenient for copulation and remained quiet (the ventral side of her abdomen turned upwards). The male commenced insertions of the palps alternatively, then again spun threads around the female and 'drummed' upon her abdomen with his palps. Each insertion lasted a few seconds only. The female remained quiet all the time and only moved her legs slowly when touched roughly by the legs of the male. Finally the insertions became more frequent and the 'swaddling' process shorter. The male appeared to have reached a state of high tension and became too careless. The female awoke seven hours and a half after the beginning of my observations and seized the male by jumping directly upon him.

Up to now the female had not reacted to any touch of the web.

One fly was placed in the web during the copulation, but remained unnoticed. Before and after copulation the female ate eagerly. The male ate only once before the copulation. In one case where the observation was stopped and the male taken away after the first insertion, both male and female ate heartily.

The 'swaddling' process by the male mainly serves to calm the female. As a matter of fact, the female can easily liberate herself from the threads spun around her by the male. It seems that not each copulation ends with the death of the male. In nature the male crawls away to a greater distance than was possible in the receptacle used for observation, and it is possible that he rests between one insertion and the other without ceasing to be on the watch.

In a temperature of 14° to 12° C. and lower, copulation does not take place.

Some physiological data.—Instantaneous thermal death occurs at 50·5° C. (see p. 315).

Other experiments were not completed owing to lack of material. As regards phototaxis, the young spiders of *L. pallidus* show the same reaction as those of *L. tredecim-guttatus*.

The amount of venom.—Lack of material and the great mortality of the young spiders during their growth did not allow extended experiments, but the first results given here may give a general outlook on the degree of venom of this species. The preliminary experiments showed that the variability of the influence of the venom is very great. A method of research similar to that used in the case of *L. tredecim-guttatus* was employed.

Summary of experiments made with venom.

Amount of venom.—

Number of animals killed when bitten successively by the same spider :—By adult female : white mice, 3 (4) ; field-mice, 4 (5), 4 (5), 0 (5), 0 (5), 2 (5), 1 (5), 1 (5). By female pre-adult : white mice, 0 (5), 0 (3).

The figures in brackets indicate the number of animals bitten.

Strength of venom.—

Number of animals killed when bitten by *L. pallidus* :—By female adult : young dogs, 0 (6) ; rabbits, 0 (2) ; guinea-pigs, 1 (2) ; white mice 1 (1) ; field-mice 6 (10). By female in adult, 1 (4). By male adult, 0 (1).

The adult spider can kill white mice, field-mice, and guinea-pigs. Rabbits and dogs suffer from the bites, but do not die. The pre-adult spider can kill white mice, but the adult male is not dangerous at all.

The symptoms are similar to those observed in the case of the *L. tredecim-guttatus* bite, viz. : heavy breathing, paralysis of the limbs, convulsions, and projecting of the head.

The conclusion to be drawn is that generally there is a decrease in the strength of the venom in successive bites, but the effect of the venom varies so much on individual animals that it can occur that the animal bitten first may remain alive, while that bitten fifth dies.

The comparative strength of the venom of both species will be discussed below.

The experiments on immunity.—The following table shows the results obtained from experiments on immunity with field mice :—

Bitten first time, 10 : number of fatal cases, 6. Bitten a second time, 12 : number of fatal cases, 1.

Owing to the great variability observed in the effect of the venom the above results are not quite conclusive. However, it may only be assumed that immunity in field-mice is developed under the influence of previous bites.

Comparative remarks.—In the following lines a parallel summary is given together with the available data concerning *L. mactans* (North American) and *L. indistinctus* (South African).

Distribution.—*L. tredecim-guttatus* is found throughout Palestine and *L. pallidus* in the plains only (Esdraelon and Jordan valleys and coastal plain Shefala). These differences are in accordance with the general distribution abroad.

The structure of the web.—*L. tredecim-guttatus* builds its web from irregular threads, while a pipe or overturned dish serves as a dwelling place. *L. mactans* spins an irregular web with

a funnel-shaped tube leading into it from a place in which the spider is concealed. The web of *L. pallidus* is a regular one, although not in the usual sense, and is composed of three parts built up in a definite order.

The cocoons of both Palestinian species differ from each other in their size (length 17 mm. against 12 mm.) and by the number of eggs (235 and 147 on the the average respectively). *L. mactans* lays 300 eggs on an average, reaching up to 771. The main period of oviposition of *L. tredecim-guttatus* falls in the winter and of *L. pallidus* in late summer and autumn. The speed of development of the former appears to be longer. In both cases the spiders remain in the sac until the completive internal changes take place (which depend upon external temperatures and humidity). The threshold of the effective temperature for leaving the sac lies between 12·3° to 14° C. and 18·4° C. respectively, and the amount of heat required for the leaving of the sac is 168 to 203 days-degrees and 104 days-degrees respectively.

The speed of development.—As a rule one to one and a half generations occur annually in both species. This fits in well with the observations on *L. mactans* in California. Under optimal conditions two generations per year may be observed.

The speed of mortality of the young spiders of both species is about equal in a temperature of 20° to 30° C., but in the low temperatures of 10° to 15° C. the first live longer. It is possible that this fact underlies differences in geographical distribution.

The food and the hunt.—L. tredecim-guttatus preys mostly on beetles and grasshoppers and *L. pallidus* on ants, though actually both can catch other prey such as woodlice, scorpions, and spiders. The mode of hunt employed by both species is similar, but the latter is aided by a special arrangement of the web and by its capacity to descend upon the victims by a special thread.

The copulation of both species is similar. The males spin threads round the female during the copulation to calm her. On *L. tredecim-guttatus* the threads are fewer, and the duration of the insertions observed in *L. tredecim-guttatus* is longer (30 seconds to 37 minutes, as against 5 to 10 seconds in *L. pallidus*).

The degree of venom.—Upon comparing the series of experiments performed with bites of both species of *Latrodectus* (*Microtus guentheri* having been experimented with) we may conclude that the venom of the former is stronger.

	In series.	First bites.	Speed of death.
L. tredecim-guttatus.	26 (34)	10 (10)	7·3 hours
L. pallidus	12 (35)	6 (10)	10·8 „

The animals experimented with reacted to the bites in a similar manner and the symptoms of the reaction were also similar.

Physiological data.—The differences in the instantaneous death-point show accordance with the geographical distribution, being in *L. tredecim-guttatus* 47·1° C. and in *L. pallidus* 50·5° C.

The young spiders of both species react similarly to both diffused light and direct sun-rays.

The *comparison between the biological facts* concerning both species shows that the differences in the speed of mortality of the young spiders at low temperatures and in the amount of heat required to leave the cocoon are the most conspicuous. These differences explain the different geographical distribution of these species. It would be very important to state experimentally the amount of venom of various *Latrodectus* species around the world.

Summary.—Some biological facts have been given concerning *L. tredecim-guttatus* and *L. pallidus* in Palestine. Their distribution and development have been dealt with. Special attention was paid to the structure of the web and the role the egg-sacs play in young spiders. The factors regulating the leaving of the sac were stated. Observations have been made on the process of copulation. The nature of the food has been investigated.

The question of the amount of venom of both species was given special emphasis, and along with some subsidiary questions an experiment was made to compare the strength of the venom of both Palestinian spiders. It has been shown that in the years in which observations were made the strength of the venom of *Latrodectus tredecim-guttatus* was greater than that of *L. pallidus*.

Acknowledgement.—The present work is the result of six years' observations and experiments on both species of *Latrodectus* spiders in Palestine. It began with Prof. U. Gerhardt's visit to Palestine, to whom I am very much indebted for inspiring me with regard to arachnological research.

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BIBLIOGRAPHY.

D'AMOUR, FRED, BECKER, FRANCIS E., & VAN RIPER, WALTER. 1936. The Black Widow Spider. *Quart. Rev. Biol.* II, no. 2.

ANCONA, LEOPOLDO H. Anatomia e histologia del aparato venenoso de *L. mactans* o arana capulina. *Ann. Inst. de Biologia*, II, pp. 77, 78.

BAERG, W. J. 1936. The Black Widow. *Bull.* 325, *Experim. Stat. Arkansas.*

BERLAND, L. 1932. Les arachnides. Paris.

BLAIR, A. W. 1934. Spider poisoning. *Arch. Int. Med.* LIV, Dec.

BLYTH, A. W., & BLYTH, M. W. 1920. Poisons, their effects and detection. 5th ed. London. Cited after 5.

CAMBRIDGE, O. P. 1872. Spiders of Palestine and Syria. *Proc. Zool. Soc.*

COMSTOCK, J. 1914. The Spider Book. New York.

FINLAYSON, M. H. 1936. Knoppie Spider Bite. *S.Afr. Med. Journ.* 25th Jan.

—— Some properties of the venom and arachnolysin of *Latrodectus indistinctus*. *S. Afr. Journ. Med. Sci.* II, no. 4, Oct.

GERHARDT, U. 1934. Neue Untersuchungen zur Sexualbiologie der Spinnen. *Zeitschr. Morphol. u. Oekologie.*

HAMBURGER, C. 1910. Die Entwicklung des Darmkanals der *Argyroneta aquatica*. *Verhandl. d. Nat. Med. Verein. zu Heidelberg.*

HERMES, W. B., BAILEY, S. F., & MCIVOR, BARBARA. 1935. The Black Widow Spider. *Univ. California, Bull.* 591, June.

PAWLOWSKY, E. 1927. Gifttiere. Leipzig.

PHISALIX, MARIE. 1932. Les animaux venimaux et venins. Paris.

REIMOSER, E. 1919. Katalog der echten Spinnen des palaearktischen Gebietes. Wien.

MOTE, DON C., & GRAY, KENNETH. The Black Widow Spider. *Oregon State Agr. Coll. Corvallis* : *Stat. Circ.* 112.

SAVORY, TH. H. 1935. The Arachnida. London.

SHULOV, A. 1937. On *Latrodectus XIII-guttatus*. Hateva vehaarez. (In Hebrew.)

—— 1936. On *Teutana triangulosa*. Hateva vehaarez. (In Hebrew.)

—— On phototaxis by young spiders. (In MS.)

TUTUNJI, D. F. 1933. A spider bite successfully treated by anti-scorpion serum. *Folia Med. Int. Orient.*

VEILLARD, J. 1936. Le venin des Aragnées. Paris.

STUDIES IN AQUILEGIA.

By MARIA SKALIŃSKA, Ph.D. (Warsaw).

HYBRIDS are freely produced in the genus *Aquilegia* when the species are brought together, but are rare in nature because, in general, the areas of the different species do not overlap or, if they do, the species are kept apart by ecological diversity, as by the occupation of different altitudes, etc. The following pages describe plants considered to be natural hybrids of *A. Reuteri* (i) with *A. alpina* and (ii) with *A. pyrenaica*, and (iii) a new species, *A. pseudalpina*.

CHARACTERS BY WHICH *A. ALPINA* LINN. AND *A. REUTERI* BOISS. ARE DISTINGUISHED.

The southern part of the geographic area of *A. alpina*, in south-eastern France, produces *A. Reuteri*, and produces

also (i) *A. vulgaris* Linn., (ii) its subspecies *A. atrata* Koch, and (iii) its variety *praecox* Jord. Of these species *A. vulgaris* and *A. atrata* grow at lower altitudes than *A. alpina*; but specimens preserved in the Herbarium of the Royal Botanic Gardens, Kew, show that *A. alpina* and *A. Reuteri* grow together in woods and on rocks in such localities as Montagne de Nanan sur Fontan in the Department of the Alpes Maritimes, Montagne Morgon, above the forest of Boscodon, and La Miolette sur Chaudun, Gap, both in the Department of Hautes Alpes; and that in these places aberrant plants occur seeming to be hybrids as they exhibit in combination characters suggesting the putative parents. Such plants have been erroneously determined as *A. alpina*.

It is desirable, before giving the description of the probable hybrids, to consider the main differences between the two parents.

Differences in the shape of the basal leaves of A. alpina *and* A. Reuteri.—*A. alpina*. Leaves biternate, with petioles 8–14 cm. long. Leaflets relatively large and broad, cuneate at base: the middle petioluled, usually 22–28 mm. long, 24–34 mm. wide, but small plants have smaller leaflets, reaching only the length of 14–18 mm. and the width of 14–19 mm.: lateral leaflets usually of unequal size, sessile; their length 18–27 mm.: their width 20–34 mm.; in the smallest plant, however, their length and width only 13 mm.; it ought to be added that these small leaflets also have the characteristic shape of *A. alpina*, which differs distinctly from all the other species. The leaflets are trilobed owing to two main deep incisions reaching at least $\frac{2}{3}$ of their length. In the middle leaflet these incisions are symmetrical, but in the lateral they are of unequal length: the external deeper than that in the half adjacent to the middle leaflet. Beside these main incisions the leaflets carry many additional incisions, which are rather broad and deep: they contribute to the dissection of the border of the leaflets producing the many long and narrow segments by which leaflets of *A. alpina* can be easily distinguished from those of any other species.

A. Reuteri.—Basal leaves biternate, with petioles 7–17 cm. long. Leaflets elongated, smaller than those of *A. alpina*, much simpler in their outlines, cuneate at the base: all sessile: the middle 10–18 mm. long, 8–14 mm. wide, and the lateral 10–13 mm. long, 8–14 mm. wide. The leaflets are trilobed; the two main incisions which contribute to form the lobes are remarkably less deep than in *A. alpina*, reaching hardly $\frac{1}{3}$ of the length of the middle leaflet. The shape of the middle leaflet is symmetrical, while the lateral leaflets are distinctly asymmetrical owing to the unequal length of these incisions: in the half adjacent to the middle leaflet

the incision is so short that sometimes the leaflet seems to be rather bilobed than trilobed. Contrary to *A. alpina* the additional incisions are very shallow and their number is low. Thus the middle leaflet carries only 3–8, the lateral ones 5–8 short rounded lobules.

Differences in the pubescence of the leaves.—In *A. alpina* the leaflets are always glabrous on both surfaces, while in *A. Reuteri* their lower surface is sparingly pubescent, carrying long and thin single unicellular hairs.

Differences in the stem leaves.—*A. alpina* has always 1–3 (usually 2) petioled stem leaves similar in shape to the basal leaves, and in addition 1–2 narrow bracts. *A. Reuteri*, in spite of the description of Rouy and Foucaud (1893), has usually no typical stem leaves, but only very narrow bracts. In rare cases the stem carries in its lower part one leaf, similar in outline to basal leaves.

Differences in the axis.—The flowering stem of *A. alpina* is thicker, 20–55 cm. high ; that of *A. Reuteri* is slender chiefly in its upper part and the peduncles are remarkably thinner ; it is 20–45 cm. high. In both species the lower part of the stem is sparingly pubescent ; its upper part, as well as the peduncles and the bracts, are somewhat glandular pubescent.

Differences in the flowers.—*A. alpina* has large blue flowers. They are about 55–95 mm. across, 30–38 mm. long. Sepals oval, broadly spreading, 25–45 mm. long, 10–20 mm. wide, exceeding the laminae by 12–25 mm. Petals with well developed subtruncate or truncate laminae and thick slightly incurved spurs : their total length 30–38 mm. : laminae 13–18 mm. long, exceeding the stamens in their length : spurs 15–20 mm. long. *A. Reuteri* has somewhat smaller blue flowers (45–60 mm. across, 23–30 mm. long). Sepals oval, acuminate, spreading, 20–26 mm. long, 10–12 mm. wide, exceeding the laminae by 9–11 mm. Petals with well developed rounded or subtruncate laminae and more distinctly incurved spurs, somewhat thinner at top than in *A. alpina* : their total length only 23–30 mm. : laminae, which are of the same length as the stamens, 11–15 mm. long, spurs 12–15 mm. long.

Putative hybrids between *A. alpina* and *A. Reuteri*.

Of four plants collected by E. Reverchon in the meadows of Montagne de Nanan sur Fontan (Alpes Maritimes) and determined as *A. alpina* one is an aberrant plant, another is true *A. alpina*, and the others are small plants of *A. Reuteri*. The aberrant plant differs in many details from *A. alpina*, as well as from *A. Reuteri*, and probably represents a spontaneous hybrid between these two species. Its description is as follows :—

Basal leaves biternate, with very long petioles (11, 17 and

19 cm.) exceeding in their length those of both putative parents. Secondary petioles 25–30 mm. long : in contrast to *A. alpina*, as well as to *A. Reuteri*, the aberrant plant has both middle and lateral leaflets petioluled. The leaflets are of intermediate size : they are smaller than in *A. alpina* and larger than in *A. Reuteri* : they seem, however, to be relatively small in comparison with their very long petioles. Middle

TABLE I, contrasting the two species.

	A. alpina.	*A. Reuteri.*
Shape of basal leaves :		
Length of petioles	8–14 cm.	7–17 cm.
Leaflets	Middle leaflet petioluled, lateral leaflets sessile.	All leaflets sessile.
Middle leaflets : length	22–28 mm.	10–18 mm.
width	24–34 mm.	8–14 mm.
Lateral leaflets : length	18–27 mm.	10–13 mm.
width	20–34 mm.	8–14 mm.
Number of lobes : middle leaflets	10–22	3–8
lateral leaflets	8–24	5–8
Main incisions	Deep, reaching at least $\frac{2}{3}$ of the leaflet's length.	Less deep, reaching only $\frac{1}{3}$ of the leaflet's length.
Pubescence : upper surface	Glabrous.	Glabrous.
lower surface	Glabrous.	Sparingly pubescent.
Stem leaves	1–3 (usually 2) similar to basal leaves.	Sometimes 1, but usually only narrow bracts.
Stem height	20–55 cm., thicker.	20–45 cm., more slender.
Flowers : length	30–38 mm.	23–30 mm.
diameter	55–95 mm.	45–60 mm.
Sepals : length	25–45 mm.	20–26 mm.
width	10–20 mm.	10–12 mm.
Petals : total length	30–38 mm.	23–30 mm.
length of laminae	13–18 mm.	11–15 mm.
length of spurs	15–20 mm.	12–15 mm.

leaflets 20–22 mm. long and 24 mm. wide ; lateral leaflets 18–20 mm. long, 20–22 mm. wide : all trilobed : the middle symmetrical ; both its main incisions nearly as deep as in *A. alpina* : associated additional incisions remarkably shorter than in *A. alpina* : those, the main and additional incisions, are to the number of 10–22. The leaflets of the aberrant plant have 5–11 lobes, while those of *A. Reuteri* have only 3–8 lobes. Lateral leaflets asymmetrical owing to a distinct difference in the length of their main incisions ; the external incision is

deeper than that in the half adjacent to the middle leaflet. Thus in size of the leaflets and number of lobes the probable hybrid is intermediate between *A. alpina* and *A. Reuteri*. Its leaves are less compound in outline than the finely incised leaflets typical of *A. alpina*.

Pubescence of the leaves.—The lower surface of the leaflets is sparingly pubescent, like *A. Reuteri* and in contrast to the glabrous leaflets of *A. alpina*.

Stem leaves.—In contrast with *A. alpina* the stem of the aberrant plant lacks typical leaves; it carries only one rudimentary leaf and two small and narrow bracts, in these characters approaching *A. Reuteri*.

The flowering stem is very tall (55 cm.), exceeding in height the typical representatives of both *A. alpina* and *A. Reuteri*, vigour being rather typical of hybrids of *Aquilegia*. In its general aspect it resembles *A. Reuteri* more than *A. alpina*, owing to the great slenderness of the upper part and to the thin peduncles which are glandular pubescent.

The flower, with its short incurved spurs, is rather similar to *A. Reuteri*. An analysis of flower-shape, however, cannot be given in detail as the only flower is much damaged. It is the characters of the vegetative parts that indicate the aberrant plant as an immediate cross-product (F_1 hybrid) of *A. alpina* and *A. Reuteri*.

Characters of a second aberrant plant.—This plant, collected by E. Reverchon in rocky woods of Ribiers (Vaucluse), is not identical with *A. alpina*, and presumably represents another hybrid whereof the second parent was possibly *A. Reuteri* likewise. The sheet holds three plants, or probably three fragments of one plant, as they seem to be identical: one carries two flowers, the others nearly mature follicles. This is a detailed description of these specimens.

Basal leaves biternate, their petioles 8–11 cm. long and secondary petioles 2–3 cm. long. Contrary to what is found in *A. alpina*, whereof the middle leaflets are petioluled, they are sessile like the lateral leaflets. Leaflets somewhat smaller than those of *A. alpina*: middle leaflets 18–20 mm. long, 20–21 mm. wide; lateral leaflets usually of unequal size, 15–18 mm. long, 11–20 mm. wide. The middle leaflets are distinctly trilobed, asymmetrical; they carry two main incisions of unequal length, the deeper of which—in contrast with *A. alpina*—does not exceed in most cases half the length of the leaflets. In the lateral leaflets, however, the asymmetry is greater: the broader of the leaflets is usually divided into two distinct parts by the deeper external incision, while the internal incision, adjacent to the middle leaflet, is conspicuously shorter. In the narrower of the two lateral leaflets

the incisions are less deep, and of unequal length. The lobes of the middle leaflets are 6–9 ; those of the broader of the lateral leaflets 7–11, the narrower only 3–9. The additional incisions are shallow, so that the lobes are rounded and the outlines of the leaflets less compound than in *A. alpina*, for they lack the very numerous deep and fine incisions typical of *A. alpina*.

Pubescence of the leaves.—The lower surface of the leaves is sparingly pubescent with long thin unicellular hairs.

Stem leaves are lacking, the stem carrying only very narrow bracts, as general in *A. Reuteri*.

Flowering stems 35–45 cm. high, in general aspect more similar to *A. Reuteri* than to *A. alpina* chiefly in their upper part, e.g. in the ramification ; and in the very thin long and slender peduncles they show a distinct similarity to *A. Reuteri*. The lower part of the stem is sparingly pubescent, the upper part as well as the peduncles abundantly glandular pubescent.

Flowers blue, about 36 mm. long and 43–50 mm. across. Sepals relatively short, oval, 19–20 mm. long, about 11 mm. wide, exceeding the laminae by only 2–3 mm. Petals with well developed laminae and relatively long spurs ; the total length 37 mm. ; that of the laminae which exceed the stamens 17 mm. : the spurs which are only slightly incurved 20 mm. long. The general shape of the flower seems to represent a combination of the well developed laminae and long spurs of *A. alpina* with the remarkably shorter sepals of *A. Reuteri*.

Follicles large (18–22 mm.), approaching in their size *A. alpina* (20–25 mm.) more than *A. Reuteri* (only 10–15 mm., according to Rouy and Foucaud), glandular pubescent. The fertility seems to be normal. The general aspect is in many details different from *A. alpina*, and is somewhat as *A. Reuteri*, so that it, too, seems to be a hybrid of these species, though by no means identical with that described first. It does not represent the immediate cross-product (F_1 hybrid), but seems to be rather a product of Mendelian segregation and recombination of characters in a later hybrid generation.

Putative hybrid between *A. Reuteri* and *A. pyrenaica*.

A third aberrant plant exists preserved in association with three other plants collected on Mont Ventoux, two being *A. Reuteri* and the third seemingly *A. pyrenaica*. All have been determined by previous workers as *A. pyrenaica* DC. Mont Ventoux belongs to the area of the geographic distribution of *A. Reuteri*, but *A. pyrenaica* has been considered to be confined to the Central Pyrenees. However, I have seen in the Kew Herbarium two typical representatives of *A. pyrenaica* DC. collected on Mont Ventoux.

I need to remark here that from the genetical point of view there is no unreasonableness in maintaining that a possibility exists of the occasional presence of plants identical with *A. pyrenaica* in areas occupied by *A. Reuteri*, for (Skalińska, 1940) I consider *A. Reuteri* and *A. pyrenaica* to be closely related species; the latter, phylogenetically younger, probably arose through gene mutations from *A. Reuteri* or from a form similar to it; the difference between them consists in such a limited number of genes that divergence could be attained through a few gene mutations followed by geographic isolation of the newly formed mutant. On the other hand, single gene mutations have led to no more than intraspecific differentiation (e.g. the dwarf form *A. Reuteri β minor* Rouy). Plants of *A. pyrenaica* found on Mont Ventoux may represent the relicts of a species which has now advanced to the south-west, as well as individuals which have arisen recently from *A. Reuteri* in the same way as the plants formed previously.

The aberrant plant from Mont Ventoux collected together with the representatives of *A. Reuteri* and *A. pyrenaica* is probably a hybrid between them. The presumed hybrid is somewhat more vigorous and differs from both parents in details of general aspect as well as flower shape. A comparison with *A. Reuteri* and *A. pyrenaica* is given in Table II.

Basal leaves in a well developed rosette: primary petioles relatively long (12–14 cm.); secondary petioles also elongated, as in *A. Reuteri*, and in contrast with the short primary and secondary petioles of *A. pyrenaica*. Leaves biternate with sessile leaflets, as in both putative parents; the shape of the leaflets intermediate: the middle leaflets of *A. Reuteri* are elongated, their length (10–18 mm.) exceeding their width (8–14 mm.); those of *A. pyrenaica* are, on the contrary, broader than long (length 8–15 mm., width 12–20 mm.), while the middle leaflets of the probable hybrid are nearly as long as wide (length 12–13 mm., width 13–14 mm.), being intermediate in both dimensions; these proportions probably result from an independent transmission to the offspring of genes for length and width. The lobes 5–10; this number is intermediate, higher than in *A. Reuteri* (3–8 lobes) and somewhat lower than in *A. pyrenaica* (6–12 lobes). The leaflets are more deeply incised than in both these species, the borders being divided into 5–10 long and rather broad obtuse segments.

Pubescence.—The probable hybrid shows slight traces of pubescence on the lower surface of the leaflets, thus being intermediate between *A. Reuteri* with sparingly pubescent leaflets and *A. pyrenaica* with glabrous leaflets.

Flowering stem slender, as in both putative parent species; its height (22 cm.) as that of the plants of *A. Reuteri* collected

with it, while *A. pyrenaica* from the same locality is only 10 cm. tall. In general in *Aquilegia* tall stem is dominant to short stem. It should be noted, however, that neither *A. Reuteri* nor *A. pyrenaica* are uniform in nature with regard to height: some representatives of *A. Reuteri* are taller, reaching 30–45 cm.; while the height of *A. pyrenaica* in its typical localities, in the Pyrenees, varies from 3 cm., for extremely small representatives of high mountain plants from Port de Benasque, to 25 cm. found in some tall plants from the Houle de la Marboré, Mont Perdu. Most frequently, however, the height of *A. pyrenaica* is 10–15 cm.

Stem leaves.—Stem in its lower part with one long petioled leaf, similar in shape to basal leaves; this detail leads to the identification of *A. Reuteri* as one parent. Though in most representatives of this species only narrow bracts are present, in some cases the stem carries a very specific long petioled stem leaf, similar in shape to the basal leaves. *A. pyrenaica* has no stem leaves.

Flower, diameter 60 mm., thus corresponding in size with *A. Reuteri* (45–60 mm.) and exceeding *A. pyrenaica* (25–55 mm.); its horizontally spreading sepals, contrasting with the less spreading sepals of *A. Reuteri*, help to exaggerate the appearance of size. Sepals relatively narrow (12 mm.), long (29 mm.) and acuminate, as wide as those of *A. Reuteri*, but somewhat longer; differing distinctly in shape from the short and broad sepals of *A. pyrenaica*, whose length is 12–23 mm. and width 9–14 mm. Though the laminae are 15 mm. long they are distinctly exceeded by the long sepals; the difference between the length of sepals and the length of laminae averages 14 mm., thus it is greater than in *A. Reuteri* in which this difference ranges from 9 to 11 mm.; and in *A. pyrenaica* with a difference of 4 to 9 mm. only. Owing to this and the wide spreading of its long sepals, the general aspect of the flower of the presumed hybrid distinctly differs from that of both species; and the shape of the petals increases the difference. *A. Reuteri* has broader laminae and thicker, shorter and distinctly incurved spurs usually with their tops closely approximated to each other, and the laminae in consequence somewhat dilated: *A. pyrenaica*, on the contrary, has very thin and nearly straight spurs; but the position of these spurs and of the laminae shows a remarkable variability, in some plants the spurs being closely approximated to each other leading to dilation of the laminae, or in others parallel to each other or somewhat spreading. The presumed hybrid has narrow laminae and relatively long slender spurs, incurved only at the apices; so that it combines the characters of incurved spurs of *A. Reuteri* with the exceedingly thin nearly straight spurs of *A. pyrenaica*. The spurs spread somewhat;

the laminae are not dilated, on the contrary their borders overlap; they are erect, orientated nearly at a right angle to the horizontally expanded sepals. The stamens of *A. Reuteri* are of the same length as the laminae, while in *A. pyrenaica* they are somewhat exceeded by the laminae; also in the presumed hybrid the stamens are included in the laminae as in *A. pyrenaica*, or perhaps to an even greater depth.

TABLE II.—Differences between *A. Reuteri*, *A. pyrenaica*, and the presumed hybrid.

	A. Reuteri.	The presumed hybrid.	*A. pyrenaica.*
Basal leaves :			
Length of petioles	7–17 cm.	12–14 cm.	2–6 cm.
Middle leaflets : length.	10–18 mm.	12–13 mm.	8–15 mm.
width..	8–14 mm.	13–14 mm.	12–20 mm.
Number of lobes	3–8	5–10	6–12
Pubescence of leaves .	Upper surface glabrous; lower surface sparingly pubescent	Upper surface glabrous; lower surface with traces of pubescence	Both surfaces glabrous
Height of flowering stem	20–45 cm.	22 cm.	3–25 cm. (usually 10–15 cm.
Stem leaves.....	Sometimes 1, similar to basal leaves, usually narrow bracts	1, similar to basal leaves	None
Flower diameter.....	45–60 mm.	60 mm.	25–55 mm.
Sepals: length	20–26 mm.	29 mm.	12–23 mm.
width	10–12 mm.	12 mm.	9–14 mm.
Position of sepals	Spreading	Widely spreading	Slightly spreading
Shape of spurs	Thick, short, incurved	Thin, longer, incurved at top	Thin, short, nearly straight
Relative length of laminae	Equalling the stamens	Exceeding the stamens	Exceeding the stamens

The above analysis of the morphological characteristics of the presumed hybrid shows that it possesses a combination of those of *A. Reuteri* and *A. pyrenaica*. A number of the characters of the first species are dominant; with regard to others the hybrid is intermediate (length and width of the leaflets, pubescence); it corresponds to *A. pyrenaica* only in its thin spurs and the long laminae which exceed the length

of the stamens : other characteristics undergo an exaggeration (e.g. wider spreading of the sepals), probably due to cooperation of the genes of both the species mentioned.

The detection of *Aquilegia pseudalpina*.

To two further gatherings of plants collected by Reverchon at the top and in the woods of Mont Ventoux, Vaucluse, I have given particular study. The first consists of nine plants, previously determined as *A. Sternbergii* Reichb. : one of them, however, is *A. pyrenaica* DC. ; another is probably a hybrid, but indeterminable, as it lacks flowers ; the remaining seven form a uniform well defined group. The second gathering consists of only three plants determined as *A. alpina* Linn. Both gatherings show a number of characters in common ; their chief difference is in size, the plants from the top of Mont Ventoux being shorter (13–25 cm.), with denser rosettes of leaves, and smaller and more pubescent leaflets ; thus they represent a mountain type. The plants from the woods are taller (27–41 cm.) : they are characterized by a more abundant development of their vegetative parts, probably owing to the external conditions (lower altitude). It is possible that the differences between the gatherings are only phaenotypic.

In spite of all my efforts I was unable to identify these rather uniform groups of plants with any of the described species of *Aquilegia* : and as they are similar to *A. alpina* in general aspect, I name them *A. pseudalpina*. They differ distinctly from that species in the shape of the leaves, the pubescence of their lower surface and the lack of stem leaves, but the shape of the flowers is similar. The determination of the first gathering as *A. Sternbergii* is erroneous, as a careful examination of descriptions of that species (Reichenbach, 1830, xxxii, p. 749 ; Zimmeter, 1875, p. 32) and of a number of herbarium specimens shows. Moreover the type-locality for *A. Sternbergii* (*A. Haenkeana* Koch) is Krain, near the river Save ; its area extends through Carinthia, Croatia and Styria, and it occurs also in the Biharia Mountains, but it has never been found in western Europe. A detailed study of specimens from Krain, as well as from Carinthia and Croatia, proved that none of them is identical with *A. pseudalpina* from Mont Ventoux. The differences between *A. Sternbergii* and the plants from the top of Mont Ventoux will now be summarized.

Why the plants from Mont Ventoux are not *A. Sternbergii*.

The petioles of the basal leaves are about 10 cm. long in *A. Sternbergii*, but in the group under consideration they

are remarkably shorter (3–6 cm.). The leaflets of *A. Sternbergii* are much larger and elongated (18–28 mm. long, 15–23 mm. wide), with larger lobes than the small leaflets (8–17 mm. long, 8–15 mm. wide) with fine incisions of *A. pseudalpina*. *A. Sternbergii* has glabrous petioles, and the petiolules as well as the lower surface of the leaflets are sparingly pubescent; the plants from Mont Ventoux have sparingly pubescent petioles and petiolules and dense pubescence on the lower surface of the leaflets. *A. Sternbergii* differs also from these plants by the presence of stem leaves, similar to basal leaves, but the stem of *A. pseudalpina* plants carries only much reduced bracts. The shape of the flowers, too, is different: in *A. Sternbergii*, more similar to *A. vulgaris* (e.g. exserted stamens), in *A. pseudalpina* similar to *A. alpina* (stamens not exceeding the laminae).

Manifestly the plants from Mont Ventoux cannot be included within *A. Sternbergii*: nor do they belong to *A. alpina*, in spite of their general similarity to it. They differ from *A. alpina* in shape of the leaves, pubescence, and lack of stem leaves; but the shape of their flowers is generally similar to that of *A. alpina*, with a not very distinctly expressed difference in the laminae. It is that in *A. alpina* the laminae are truncate, or in rare cases subtruncate, usually with a faint incision at their top, while in *A. pseudalpina* they are subtruncate or rounded and always without the incision at the top.

Characters of plants from the top of Mont Ventoux.

The shape of the leaves.—Petioles 3–6 cm. long. Leaves in most cases not exactly biternate, their leaflets usually fused at the base; thus, each secondary petiole carries only one deeply trilobed leaflet, each of its lobes corresponding to one leaflet of *A. alpina*. The lobes have a small number of short incisions which form 3–6 lobules on the middle lobe. The lateral lobes are often of unequal size and have 3–8 lobules. The shape of the leaflets of *A. pseudalpina* differs distinctly from that of *A. alpina*, which is characterized by a very large number (8–24) of narrow segments formed by deep incisions. They are small, but with a large range of variability: those of *A. alpina* being larger (22–28 mm. long, 24–34 mm. wide). The middle and lateral lobes (which correspond to the leaflets of *A. alpina*) are of the following sizes:—middle lobes: length, 8–17 mm.; width, 8–15 mm.: lateral lobes: length, 8–13 mm.; width, 8–13 mm.

Pubescence.—The leaflets of *A. alpina* are always glabrous on both surfaces, but *A. pseudalpina* has pubescent leaves. In most of the plants the petioles and petiolules are only sparingly pubescent, while the lower surface of the leaflets is

densely pubescent, bearing long and thin unicellular hairs. One of the plants, however,—namely a plant with a very dense rosette of leaves—has abundantly pubescent petioles and petiolules, with two kinds of unicellular hairs—long and thin hairs, as well as shorter glandular hairs, broad at their base and very thin in their upper part. It should be noted that such glandular hairs are present in most species of *Aquilegia* (including *A. alpina*) on the upper part of the stem, especially on the peduncles. They are present also in all the *A. pseudalpina* plants.

Stem leaves are lacking in *A. pseudalpina* in contrast to *A. alpina*, the stem of which bears 1–3 (usually 2) leaves, similar in shape to the basal leaves. Of the seven *A. pseudalpina* plants, only one has a very small rudimentary stem leaf, while all the others carry exclusively small narrow bracts.

Characters of plants from the woods of Mont Ventoux.

The shape of the leaves.—Petioles 7–11 cm. long: most of the well-developed basal leaves biternate, nevertheless in some the leaflets fused at the base, as those of the plants belonging to the other group. Leaflets cuneate at the base: the middle leaflet trilobed, with a limited number of additional fine incisions, less deep than those of *A. alpina*. The lateral leaflets carry one main incision which reaches half of their length, and a limited number of additional fine incisions. The total number of lobules formed by these incisions is, for the middle leaflet, 7–10, and for the lateral ones 8–11. This number is lower than in *A. alpina*, and the incisions are remarkably more shallow; thus, the lobes and lobules of *A. pseudalpina* are round, in contrast with the narrow elongated ultimate segments of *A. alpina*. The leaflets are smaller than those of *A. alpina*, but they are larger than those of the plants from the top of Mont Ventoux. The middle leaflets are 14–18 mm. long and 18–20 mm. wide. The lateral leaflets are 13–18 mm. long and 18–20 mm. wide. It ought to be mentioned that in *A. alpina* the middle leaflet is in most of the specimens remarkably larger than the lateral ones (see Table I), while in these plants all three leaflets are approximately of the same size.

Pubescence.—Like the other group and in contrast with *A. alpina*, the petioles and petiolules are sparingly pubescent; the lower surface of the leaflets, however, is less pubescent than in the plants from the top of Mont Ventoux. The petioles bear here, besides the long and thin hairs, a small quantity of glandular hairs.

Stem leaves.—Only the smallest plant (27 cm. high and without basal leaves) possesses a stem leaf. In both the

other plants (which are 41 cm. and 29 cm. high) stem leaves are lacking, and only small narrow bracts are present.

The comparison between the groups of plants from Mont Ventoux leads to the conclusion that there are no essential differences between them. The differences are rather quantitative, concerning the height of the flowering stem and the size of the leaves. Their flowers have the same shape, closely similar to that of *A. alpina*. While the first group of plants shows a similarity to the smallest plants of *A. alpina* from high altitudes, the second group corresponds more to the taller plants of *A. alpina*, for instance, to those collected by Reverchon in the meadows of Grangette, Mont Aurouse, Gap.

Characters of certain plants from the Alpes Maritimes.

A specimen of *Aquilegia*, collected by Reverchon in the woods of Saint Martin d'Entraunes (Alpes Maritimes) must be taken into consideration. It has been determined as *A. viscosa* Gouan—erroneously in my opinion, as the shape of the flowers shows that it certainly does not belong to that species. It is a further representative of the "*pseudalpina*" group. The gathering is of two plants: one in flower, 50 cm. high, and one with follicles, 38 cm. high. These plants, especially the first, show striking similarity to the group of plants collected in the woods of Mont Ventoux and to the taller plants of *A. alpina*.

The shape of the leaves.—Petioles 5–11 cm. long. Basal leaves well developed, biternate, with leaflets of the same shape and size as those of the second "*pseudalpina*" group, cuneate at the base; the main incisions not as deep as in *A. alpina*. The total number of lobules formed by the main incisions and the additional ones in the middle leaflets is 8–16, in the lateral leaflets, 6–13. The middle leaflets are 15–18 mm. long, 15–20 mm. wide. The lateral leaflets are 13–17 mm. long and 17–20 mm. wide.

Pubescence: the petioles and petiolules, as well as the lower surface of the leaves, are sparingly pubescent.

Stem leaves: the flowering plant has one rudimentary leaf in the lower part of its stem, and the second plant lacks stem leaves.

Flowers: in shape distinctly similar to the plants from the woods of Mont Ventoux, though the flower is somewhat larger (see Table III).

It is to be noted that although this flower apparently seems to have longer spurs, such a difference does not exist, being due to an accidental misplacement of broken spur fragments of the dried specimen.

Definition of *A. pseudalpina*.

The above detailed analysis shows that *A. pseudalpina* is composed of a group of plants well-defined by a number of common morphological characteristics, and is so well-marked from that species with which it seems to be closely related, namely *A. alpina* L., as to deserve recognition as a species.

I name it *A. pseudalpina*. Within the limits of its definition there are forms differing from each other, like the extreme types of *A. alpina* when they grow in different localities. The first represents a mountain form, while the second is a form from lower altitudes. A Latin diagnosis of this new species follows.

Table III.—Differences between "*pseudalpina*" plants.

Localities :	Top of Mt. Ventoux.	Woods of Mt. Ventoux.	Alpes Maritimes.
Length of petioles	3–6 cm.	7–11 cm.	5–11 cm.
Middle leaflets :			
length	8–17 mm.	14–18 mm.	15–18 mm.
width	8–15 mm.	18–20 mm.	15–20 mm.
Lateral leaflets :			
length :	8–13 mm.	13–18 mm.	13–18 mm.
width	8–13 mm.	18–20 mm.	17–20 mm.
Number of lobes :			
middle leaflets	3–6	7–11	8–16
lateral leaflets	3–8	8–11	6–13
Height of flowering stem	13–25 cm.	27–41 cm.	38 and 50 cm.
Flowers :			
diameter	55–60 mm.	60–68 mm.	80 mm.
Sepals :			
length	24–27 mm.	30–34 mm.	38 mm.
width	14–15 mm.	17 mm.	18 mm.
Petals :			
length	27–30 mm.	28 mm.	30 mm.
Spurs :			
length	14–15 mm.	16 mm.	16 mm.
Flowering time	July	June	End of May

Aquilegia pseudalpina, sp. nov., cum *A. alpina* Linn. confusa, et illam floribus simulans, sed foliorum forma magnitudine necnon pubescentia, praeterea foliis caulinis valde reductis bracteiformibus distincta.

Folia radicalia biternata vel ternata ; foliola triloba incisa, parva lobo medio 8–18 mm. longo, supra glabra, subtus puberula. *Folia caulina* bracteiformia. *Caulis* firmus, apicem versus puberulus 1–4-florus. *Flos* magnus caeruleus. *Sepala* ovata longa. *Calcaria* uncinata lamina petalorum longiora. *Stamina* lamina petalorum breviora.

α forma *major*. *Foliola* crebre incisa, lobo medio 14–18 mm. longo. *Caulis* 25–50 cm. altus. *Sepala* 30–38 mm. longa.

β forma *minor*. *Folia radicalia* breviter petiolata, ternata ; foliola minora, lobo medio 8–17 mm. longo, subtus dense puberula. *Caulis* saepe uniflorus 13–25 cm. altus. *Sepala* 24–27 mm. longa. *Calcaria* uncinata lamina petalorum aequilonga.

Most of the well developed basal leaves are biternate, nevertheless the leaflets may be fused at the base, thus becoming more or less ternate. The leaflets are small (the middle leaflets 8–18 mm. long), cuneate at the base. The petioles and petiolules, as well as the lower surface of the leaflets, are sparingly pubescent. The stem lacks well developed leaves and bears only small and narrow bracts : it is rather robust, glandular pubescent in the upper part, bearing 1–4 flowers. Flowers large, blue : sepals large, widely spreading : spurs thick, slightly incurved, they exceed usually the laminae in length ; the laminae are longer than the stamens so as to include them.

α forma *major*. Petioles of the basal leaves 5–11 cm. long. The middle leaflet is 14–18 mm. long, 17–20 mm. wide ; it is trilobed owing to two main incisions, while the lateral leaflets have only one deep incision which reaches to half their length. The borders of the leaflets bear fine and narrow additional incisions which form 7–16 lobules in the middle leaflets, and 6–13 lobules in the lateral ones. The stem is 25–50 cm. high. Flower in diameter 60–80 mm. ; sepals 30–38 mm. long, 17–18 mm. wide ; the total length of the petals 28–30 mm., the spurs are about 16 mm. long. Flowering time : in the second half of May and in June.

β forma *minor*. Petioles of the basal leaves only 3–6 cm. long. The basal leaves are ternate. The leaflets are smaller and the number of lobes is lower (3–8) than in forma *major*. The lower surface of the leaflets is densely pubescent. The flowering stem is short, 13–25 cm. high, bearing usually only one flower. Flower diameter 55–60 mm. ; sepals 24–27 mm. long, 14–15 mm. wide ; the total length of the petals 27–30 mm., the somewhat more incurved spurs being 14–15 mm. long, thus of the same length as the laminae. Flowering time is later than in forma *major* (July), probably owing to difference in altitude.

Localities.—Forma *major* : Mont Ventoux (Vaucluse), Saint Martin d'Entraunes (Alpes Maritimes), growing in woods ; forma *minor* : top of Mont Ventoux.

It seems probable that a number of herbarium specimens from the mentioned localities, and also from other localities in the Alpes Maritimes, primarily determined as *A. alpina* Linn. in reality represent *A. pseudalpina* ; thus plants from the southern limit of the area of *A. alpina* deserve further studies,

as the problem arises whether in these localities *A. alpina* occurs growing together with *A. pseudalpina* or whether it is replaced there by this last species.

Table IV summarizes the character differences between *A. alpina* and both forms of *A. pseudalpina*.

TABLE IV.—Character differences between *A. alpina* and *A. pseudalpina*.

	A. alpina.	*A. pseudalpina.*	
		forma major.	forma minor.
Shape of the basal leaves	biternate	biternate or ternate	ternate
Length of petioles	8–14 cm.	5–11 cm.	3–6 cm.
Middle leaflets : length.	22–28 mm.	14–18 mm.	8–17 mm.
width.	24–34 mm.	15–20 mm.	8–15 mm.
Lateral leaflets : length.	18–27 mm.	13–18 mm.	8–13 mm.
width.	20–34 mm.	17–20 mm.	8–13 mm.
Number of lobes :			
middle leaflets	10–22	7–16	3–6
lateral leaflets ...	8–24	6–13	3–8
Incisions of the leaflets	deep and broad	much shorter and narrow	much shorter and narrow
Pubescence of the leaflets	both surfaces glabrous	lower surface sparingly pubescent	lower surface pubescent
Stem leaves.....	1–3 (usually 2) similar to basal leaves.	Only narrow bracts.	Only narrow bracts.
Height of the flowering stem	20–55 cm.	27–50 cm.	13–25 cm.
Flowers : diameter ...	55–95 mm.	60–80 mm.	55–60 mm.
Sepals : length	25–45 mm.	30–38 mm.	24–27 mm.
width.....	10–20 mm.	17–18 mm.	14–15 mm.
Petals : total length ..	30–38 mm.	28–30 mm.	27–30 mm.
Spur length	15–20 mm.	16 mm.	14–15 mm.

It is impossible, of course, to elucidate on no more than morphological criteria the genetic value of these differences between the forms within the new species ; it may be they are only phaenotypic : it is possible, however, that they represent genic differences, like the diverse types which often exist within the limits of a coenospecies. Only studies of living plants in their native localities and experiments in transplanting them to other altitudes can throw light on this problem.

PHYLOGENETIC CONSIDERATIONS.

The problem now arises to which of the known species *A. pseudalpina* is most closely related.

extreme case, *A. nigricans*, they exceed the laminae by 8–9 mm. The opposite direction of development is represented by an enlargement of the laminae which leads to the stamens being inserted. A number of species, which represent derived forms, show a gradually increasing length of the laminae. In *A. Reuteri* the laminae are only slightly longer than in the primitive type. They are of the same length as the stamens. In *A. alpina* and also in *A. pseudalpina* the laminae exceed the stamens by about 2 mm. A gradual increase of the length of the laminae is observed in *A. Einseleana*, *A. pyrenaica* and *A. Kitaibelii*. In these species the laminae exceed the stamens by 3, 4 and 5 mm. The extreme forms, however, are represented by the species *A. Bernardi* Gren. & Godr., *A. transsilvanica* Schur and *A. aurea* Jka. with greatly elongated laminae, which exceed the inserted stamens by 9 mm., 9 mm. and 11 mm. respectively.

The spurs of the more primitive European species, *A. vulgaris*, as well as its closely related species (*A. Sternbergii*, *A. atrata* and *A. nigricans*) are 14–18 mm. long. In the derived species the spurs manifest little diversity in their shape and size, showing in most cases a tendency to reduce their length rather than to increase it. A distinct reduction in the length of the spurs can be observed in *A. Kitaibelii*, *A. pyrenaica*, and *A. Bernardi*. All these species have thin, short, and nearly straight spurs, and relatively long laminae. The spurs of *A. transsilvanica* are also short, but they are distinctly incurved, contrary to the straight spurs of the above-mentioned species.

A. alpina is rather unique amongst the derived European species in its tendency to increase somewhat the length of the spurs. They are rather thick, 15–20 mm. long, usually only slightly incurved. It ought to be added, however, that the characters of shape and length of the spurs show a remarkable variability. In some plants the spurs are shorter and more incurved, whilst in others they are longer and only slightly incurved. *A. pseudalpina* shows a striking similarity to *A. alpina* with regard to the form of the spurs and also to their variability. Plants from the top of Mont Ventoux have shorter and more incurved spurs than those from both the other localities.

The above comparison of a number of characters of European species with the new species described by me leads to some conclusions concerning the problem of its origin.

Like *A. alpina*, *A. pyrenaica*, *A. Reuteri*, *A. Einseleana* and *A. Kitaibelii*, *A. pseudalpina* also seems to represent a derived species. In some of its characters it is closely similar to *A. alpina*, it has evidently followed in its specialization the same direction as this species (size of the sepals and the wide spreading of them, shape of the spurs, and length of the

laminae). In other characters, however, it shows a specialization in a direction quite different from that of *A. alpina* (reduction of the stem leaves, reduction of the size of the leaflets, pubescence). Thus, generally speaking it represents a combination of vegetative parts of small-leaved mountain species with the flowers of *A. alpina*, in other words, it combines groups of characters of two different main lines of development of derived species. This leads to the suggestion of its possible hybrid origin. This species could arise by interspecific hybridization of *A. alpina*, or some ancestor of it, with a small-leaved mountain species, followed by the production of one or two closely related types combining some of the characters of the parent species. The morphological delimitation of *A. pseudalpina* is as distinct from *A. alpina* as from the small-leaved mountain species.

As mentioned previously, the new species *A. pseudalpina* shows a differentiation into two forms: that from lower altitudes—forma *major*—seems to be phylogenetically older than the forma *minor* which represents a more extremely specialized mountain form; according to Payson the small ternate leaves of some mountain American species arose in consequence of the reduction of biternate leaves; his opinion agrees with my general conclusions concerning European species.

The studies on which this paper is based were carried out in the Herbarium of the Royal Botanic Gardens, Kew. I wish to express my deep indebtedness to Sir Arthur Hill, the Director of the Royal Botanic Gardens, and to Mr. A. D. Cotton, the Keeper of the Herbarium and Library, for the possibility to continue my research work away from Poland. My sincere thanks are also due to Dr. W. B. Turrill and Mr. N. Y. Sandwith for their valuable suggestions and their kind assistance in the final preparation of the English manuscript.

Literature cited.

Anderson, E., & Schafer, B. 1931. Species hybrids in *Aquilegia*. *Ann. Bot.* xlv, pp. 633–45.

Baker, J. G. 1878. A synopsis of the known forms of *Aquilegia*. *Gard. Chron.* Ser. 2, x, pp. 18–20, 76, 111 and 203.

Payson, E. B. 1918. The North American species of *Aquilegia*. *Contrib. U.S. Nat. Herb.* xx, pp. 133–55.

Reichenbach, H. G. 1830. Fl. Germanica, xxxii, p. 749.

Rouy, G., & Foucaud, J. 1893. Flore de France.

Schott, H. 1853. Ueber Aquilegien. *Verhandl. Zool. Botan. Vereins Wien*, iii, pp. 125–130.

Skalińska, M. 1940. Studies in phylogeny of European species of *Aquilegia* (in the press).

Zimmeter, A. 1875. Verwandtschafts-Verhältnisse und geographische Verbreitung der in Europa einheimischen Arten der Gattung *Aquilegia*. Steyr.

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